

Effects of a localized supply of H_2PO_4 , NO_3 , Ca and K on the concentration of that nutrient in the plant and the rate of uptake by roots in young maize plants in solution culture

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Summary

The effects of localizing the supply of H_2PO_4 , NO_3 , Ca or K on the concentrations of these nutrients in the plants and on the rate of uptake by the roots was studied experimentally in plants of *Zea mays* with a divided root system by frequent plant sampling.

Restricting the supply of a nutrient to one of four roots (treatment) resulted in a concentration in the shoot of that nutrient laying somewhere between that in the supplied and that in the non-supplied control plant. The calculated rate of uptake by the roots ($\text{mmol g}^{-1} \text{ day}^{-1}$) of the locally supplied nutrient was higher in the supplied root of the treatment ($+R_L$) than in those of the +control plant ($+R_c$). This negative relationship between nutrient concentration in the shoot (and sometimes also nutrient concentration in the root) and the rate of nutrient uptake in the root indicates the existence of a negative feedback control by the concentration in the shoot on the rate of uptake in the root directed unto a desired level in the shoot. The possible nature of the controlling signal is discussed.

Increase in content of locally supplied nutrient in non-supplied roots, especially in the treated plants but also in the -control plants, indicates a net flux of nutrients from shoot to root. This flux concurs in non-supplied plants with decreasing shoot-root ratio and in treated plants with restored growth rate of the non-supplied roots.

Total cation concentration ($\text{K} + \text{Na} + \text{Ca} + \text{Mg}$) was remarkably independent of treatment and kind of tissue, but Na and Mg contributed more in the root and Mg more in the shoot at K deficiency.

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Introduction

When in young maize plants in solution culture the supply of either H_2PO_4 , NO_3 , Ca or K is limited to only part of the roots while all other nutrients are available to all of them, the production of dry matter and its distribution among shoot and roots remains essentially unaltered. Within the root system, however, temporary changes in dry matter distribution do occur resulting in increased ratio of supplied root weight to total root weight (de Jager, 1982). This partly compensates for the lower uptake of the locally supplied nutrient at the beginning of the experiment, if rate of uptake is assumed to be at least unimpaired, and provides part of the explanation for the observed normal dry matter production in the treated plant.

A second type of compensation that is expected to occur at the same time is the stimulation of the rate of net uptake per unit weight, surface or length of root.* This has been observed for instance by Goedewaagen (1942) and Drew & Saker (1978) for H_2PO_4 , by Drew & Saker (1975) and Frith & Nichols (1975) for NO_3 , by Lean et al. (1974) for K, by Barta (1976) for NH_4 and NO_3 , and by Gile & Carrero (1917) for H_2PO_4 , NO_3 , K and Fe. Both the stimulation of rate of root growth and the stimulation of rate of uptake are observed in solution culture as well as in soil. In soil, a third type of compensation might play a role at the same time, i.e. alteration of length or surface per unit weight of root (thinner roots) (Goedewaagen, 1942). The relative importance of this type of compensation probably depends on the concentration of the nutrient in solution which would determine whether root volume (fresh weight) or root length or surface may become a limiting factor for the rate of uptake. In solution culture with a high concentration of the nutrients this may be the root volume as dominated by cortex volume (see Petterson, 1975) while at low concentrations, as prevailing in the soil, root surface may, in general, be the most important parameter.

In this paper we present the results of experiments that are aimed at a more precise description of the changes in the rate of uptake after localizing the supply of a nutrient, and the relation of these changes to the concentration of that nutrient in the plant tissues.

Materials and methods

Details concerning experimental procedures and cultivation conditions have been described in a previous paper (de Jager, 1982). The conditions during the pre-treatment period and the experiments were as follows: illumination by fluorescent light at 60 W m^{-2} , 16 hours at 28°C and 30 % RH, and 8 hours dark at 24°C and 45 % RH. During the pre-treatment period the nutrient to be supplied locally later on was excluded from the nutrient solution in the H_2PO_4 and K treatment but included in the NO_3 and Ca treatment. Plants to be treated had four crown roots, one of which was placed in a compartment with a complete nutrient solution and three in a

* Though increase in rate of uptake may be interpreted as stimulation of influx, derepression of influx or even repression of efflux, we will continue to describe the effect simply as stimulation of rate of uptake.

compartment containing a solution in which one nutrient was absent. All roots of the control plants were placed in one compartment containing either a complete solution (+control) or a solution without the nutrient under investigation (-control). A number of treated plants and control plants was harvested at regular time intervals (mostly every one or two days), roots were rinsed in tap water, shoots and roots were weighed, dried at 70 °C (NO₃ treatment) or 90 °C (other treatments) and weighed again. Dry shoot and root material was ground to powder with a grinder (type Retsch ZM1). Further details are presented in the legend to Fig. 1.

The total amount of P, K, Na, Mg and Ca in the plant material was determined after dry ashing at 550 °C, P colorimetrically (molybdenum-blue method) and K, Na, Mg and Ca by atomic absorption spectrometry. NO₃ was determined with an ion-specific nitrate electrode (type Orion 92-07) in an aqueous extract of dry material according to a standard procedure involving the addition of KH₂PO₄ to a concentration of 0.1 mol dm⁻³ and the addition of some Al-saturated resin (Slangen & Hoogendijk, 1970). This method seems rather reliable since we found hardly any NO₃ in plant tissues that we knew to be N-deficient. Organic N was determined by the Kjeldahl method. Since recovery of N was not complete (95 %) and NO₃ was found to be included to some extent in the determination (though no salicylic acid was added), a slight overestimation resulted for N-rich material (relatively high NO₃ content) and a slight underestimation for low-N material (no NO₃). For this phenomenon no corrections were made. Total N was computed by adding N-organic and NO₃.

The rate of uptake of a nutrient per unit root mass was calculated on the basis of two assumptions:

(a) the rate of uptake per plant is proportional to root mass:

$$dM/dt = U \cdot R \quad (1)$$

where M is the total amount of nutrient in the plant (mmol), t is the time (day), R is root weight (g) and U represents the rate of uptake per gram of root (mmol g⁻¹ day⁻¹).

(b) The root growth is exponential:

$$R = R_1 \cdot e^{k(t-t_1)} \quad (2)$$

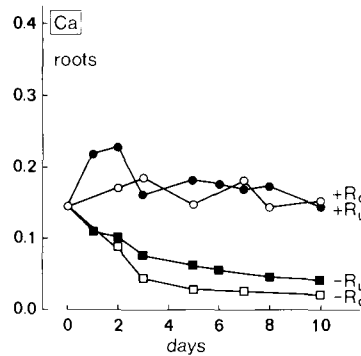
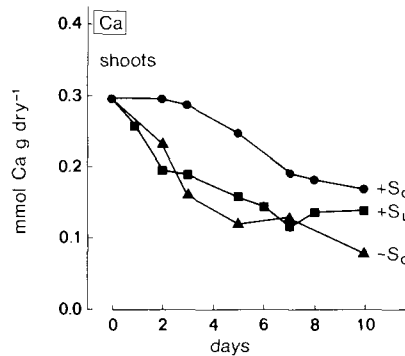
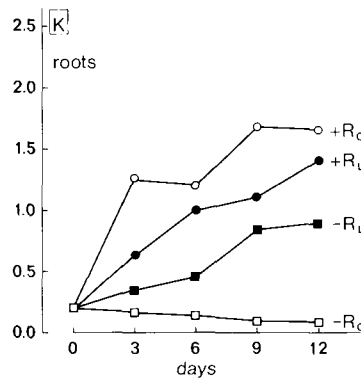
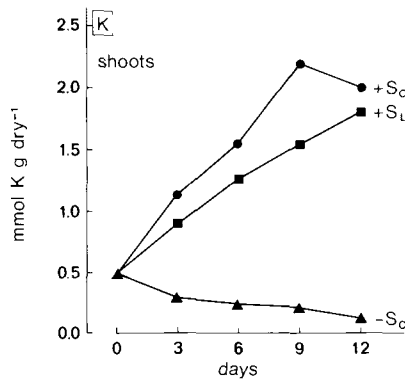
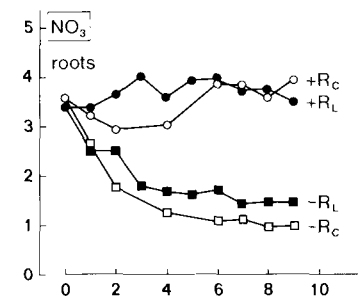
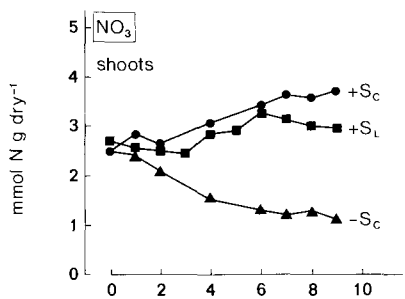
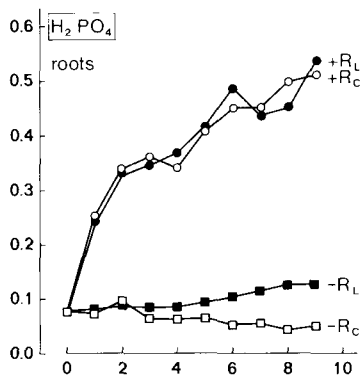
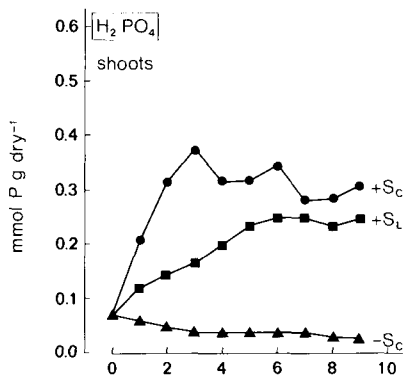
where k is the relative growth rate of the roots (g g⁻¹ day⁻¹) and R_1 is root weight at $t = 1$.

Substituting (2) into (1) gives

$$dM/dt = U \cdot R_1 \cdot e^{k(t-t_1)} \quad (3)$$

which upon integration between instant 1 and 2 yields

$$U = \frac{M_2 - M_1}{t_2 - t_1} \times \frac{\ln R_2 - \ln R_1}{R_2 - R_1} \quad (4)$$



Eq. 4 has been presented first by Williams (1948) and can be used to deduce mean rate of uptake per gram of root between two measuring dates.

The assumption of constant growth rate ($R = R_1 + y \cdot t$) turns the right half of the right term in Eq. 4 into $(R_1 + 1/2y(t_2 - t_1))^{-1}$ where y is the daily weight increase of roots (g day^{-1}), and this part of the term approaches $1/R_1$ for constant root weight.

Results

Fig. 1 shows the P, N, K and Ca concentrations in the shoots (left) and roots (right), both in the controls (uniform supply) and the treatment (localized supply). Note that in the experiment with localized H_2PO_4 and K the plants started with a low concentration of these nutrients due to their exclusion from the solution during the pre-treatment.

Shoots of the treated plants ($+S_L$) always had a lower concentration of the locally supplied nutrient than shoots of the supplied control plant ($+S_c$), but a higher concentration than shoots of non-supplied control plants ($-S_c$). The only exception to the latter was the Ca concentration in $+S_L$ that only after 8 days was higher than that in the $-S_c$.

Comparison of the (total) concentration of the locally supplied nutrients of the supplied root of the treatment ($+R_L$) and those of the supplied control ($+R_c$) reveals no general pattern. The P concentration was similar in both root types, the K concentration was lower in $+R_L$, and the N and Ca concentration at first higher in $+R_L$ and later similar in both root types.

Like in the corresponding shoot, the concentration of the omitted nutrient in the non-supplied roots of the $-$ control plants ($-R_c$) decreased steadily, while in the non-supplied roots of the treatment ($-R_L$) it decreased less (Ca and NO_3 treatment) or even, after some time, increased (H_2PO_4 and K treatment).

Since we were investigating possible relations between rate of uptake and internal concentration, in the NO_3 treatment the NO_3 concentrations in the plant tissues were of particular interest. Table 1 shows that, generally, NO_3 concentrations are lower in the $+S_L$ than in the $+S_c$ and also lower in the $+R_L$ than in the $+R_c$, at least during the second half of the experiment. It is also apparent that the NO_3 concentration in $-R_L$, after a rapid initial fall, remains at a higher level than that in $-R_c$, although both levels are very low and some measuring error could be involved.

The calculated rate of uptake of the locally supplied nutrient ($\text{mmol per g dry per day}$) by the roots of the treatment and of the $+$ -control are compared in Fig. 2. Generally the rate of uptake appears to be stimulated in $+R_L$. As judged by the mean

Fig. 1. The effect of localizing the supply of single nutrients on concentrations of that nutrient in the shoot (left) and root (right) (mmol per g dry) for H_2PO_4 , NO_3 , K and Ca.

Control plants (shoots $+S_c$ or $-S_c$) had all their roots ($+R_c$ or $-R_c$) in a complete nutrient solution or in a solution lacking one of the nutrients. Treated plants (shoot, $+S_L$) had one root ($+R_L$) in a complete nutrient solution and three roots ($-R_L$) in a solution lacking one of the nutrients. Values are the means of 2-6 individually analysed plants (P and N) or the means of two replicate analyses of 2-6 pooled plants (K and Ca).

Table 1. NO_3 concentration (meq per g dry) in shoots and roots of the treated plant and the controls, after starting the localized supply of nitrate. For symbols, conditions and replication see legend to Fig. 1.

Day	Shoots			Roots			
	$-S_c$	$+S_c$	$+S_L$	$-R_c$	$-R_L$	$+R_c$	$+R_L$
0	0.21	0.21	0.25	0.81	0.63	0.81	0.63
1	0.16	—	0.25	0.36	0.26	0.90	0.32
2	0.12	0.26	0.33	0.12	0.14	0.65	0.78
3	—	—	0.22	—	0.09	—	0.76
4	0.07	0.44	0.37	0.05	0.09	0.79	1.02
5	—	—	0.43	—	0.12	—	0.96
6	0.06	0.55	0.54	0.06	0.15	1.34	0.96
7	0.04	0.74	0.61	0.04	0.09	1.26	0.91
8	0.06	0.78	0.54	0.04	0.11	1.15	0.94
9	0.06	0.78	0.53	0.03	0.07	1.44	0.85

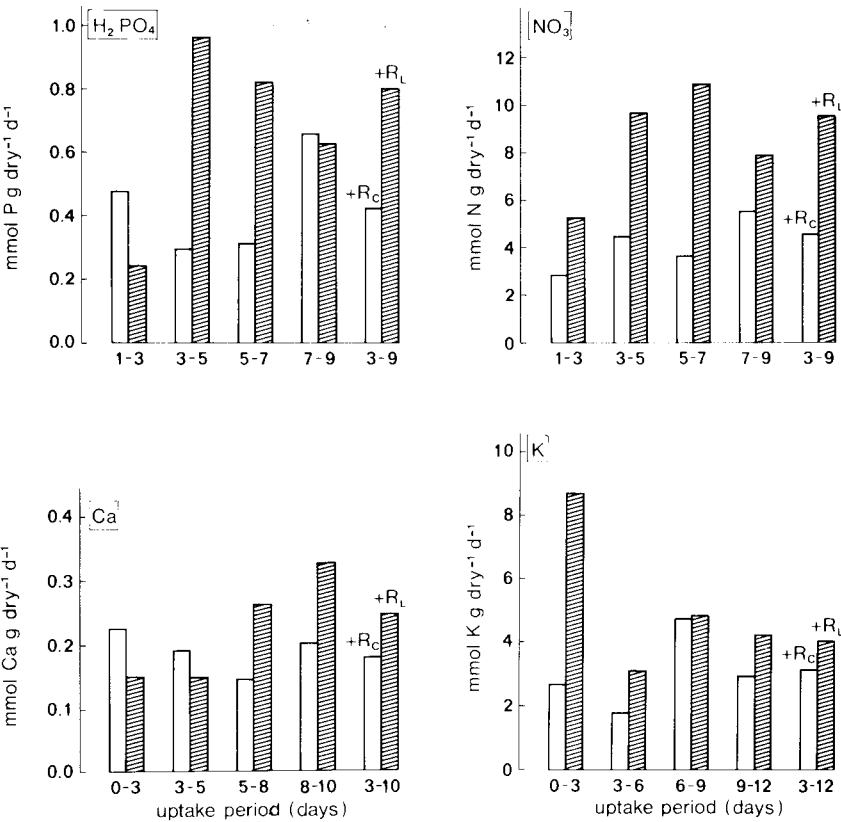


Fig. 2. The effect of localizing the supply of a single nutrient on the rate of uptake (mmol per g dry per day) by supplied roots of control (open bars) and treated plants (shaded bars), in the case of H_2PO_4 , NO_3 , K and Ca localization. The bars represent values over the indicated periods that are calculated using dry weight and concentration data. The last pair of bars represents the arithmetic mean of the three preceding values. For further details see legend to Fig. 1.

rate of uptake (last pair of bars), from which the results of the first period are omitted because there are less accurate, this effect seems to be most pronounced for H_2PO_4 and NO_3 . Stimulation of Ca uptake seems to require several days to become apparent. The figures suggest a maximum in the rate of uptake of H_2PO_4 and NO_3 but the data are not conclusive because of the restricted duration of these experiments.

From root weight and nutrient concentration in the root, the total amount of nutrient in the root (nutrient content, $\mu\text{mol root}^{-1}$) is calculated for the $-R_L$ and the $-R_c$ the results of which are presented graphically in Fig. 3. From this it is apparent that in all treatments the content of the omitted nutrient increases in the $-R_L$, indicating a net internal transport to these roots from the other plant parts. This seems to be true even for the rather phloem-immobile Ca, and this net increase in nutrient content seems to occur also in the roots of the non-supplied control plants.

In one of the experiments on the effects of a localized K supply especially the stimulation of root growth in the treated plant was far less than in the experiment

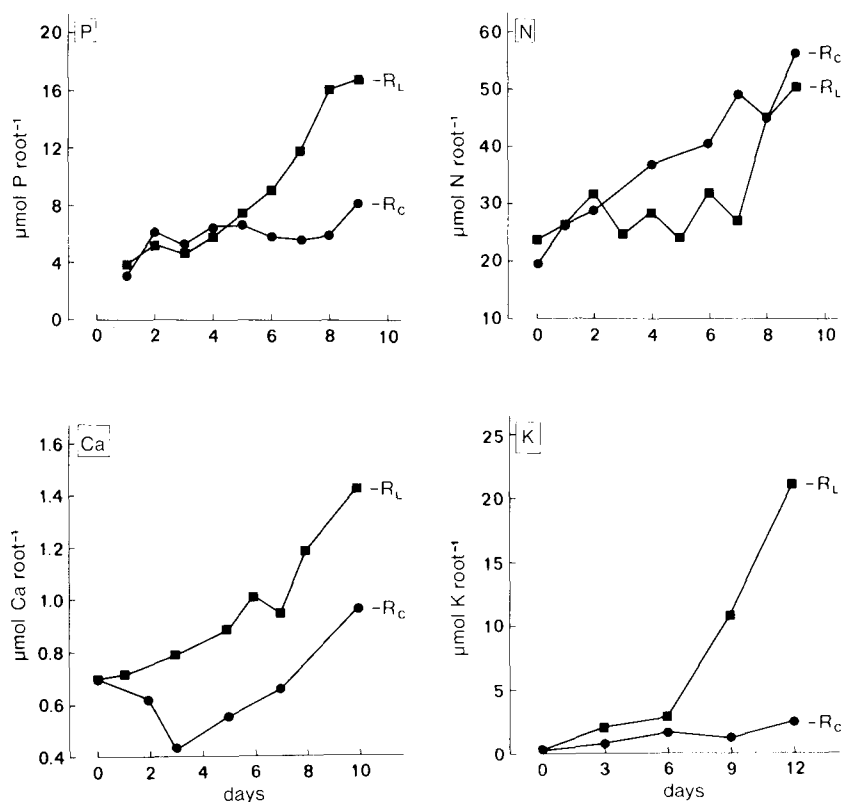


Fig. 3. The content of single nutrients of roots of control plants ($-R_c$) and treated plants ($-R_L$) that had no external supply of that nutrient; treatment indicates a localized supply of that nutrient to one of four crown roots of one plant. For further details see legend to Fig. 1.

Table 2. Single and total cation concentration (meq per g dry) of shoots and roots of the treated plant and the controls, 15 to 16 days after starting the localized supply of potassium. In the deficient nutrient solutions KNO_3 was replaced by a mixture of NaNO_3 , $\text{Mg}(\text{NO}_3)_2$ and $\text{Ca}(\text{NO}_3)_2$. For symbols, conditions and replicate numbers, see legend to Fig. 1.

Cation	Shoots			Roots			
	$-S_c$	$+S_c$	$+S_L$	$-R_c$	$-R_L$	$+R_c$	$+R_L$
K	0.32	0.93	0.89	0.19	0.23	1.25	0.93
Na	0.08	0.37	0.28	0.47	0.47	0.12	0.13
Mg	1.14	0.26	0.50	0.94	0.82	0.26	0.18
Ca	0.52	0.36	0.30	0.46	0.40	0.30	0.22
total	2.06	1.92	1.97	2.06	1.92	1.93	1.46

reported here, which could be explained by contamination of the K-deficient nutrient solution. However, some data on the cation balance may be presented here since they show how the omitted K was replaced in low-K tissue. Table 2 only shows this balance at the end of the experiment since no substantial changes occurred with time. There appears to be a remarkable constancy in total cation concentration ($\text{K} + \text{Na} + \text{Mg} + \text{Ca}$) at a value of about 2 meq per g dry, independent of the presence of K, with only one exception (a value of 1.46 meq per g dry for $+R_L$). Although K concentration in the $+S_L$ is about the same as in the $+S_c$ (0.89 and 0.93 meq per g dry respectively) yet the Mg concentration is evidently increased while Ca and Na concentration seem to be decreased. This is correlated with the high Mg concentration in the $-R_L$. In the $-S_c$ K is evidently replaced mainly by Mg and only little by Ca. Note the very low Na concentration in this shoot which is in contrast with the situation in the corresponding root ($-R_c$). For the roots the most important factor seems to be the composition of the outside nutrient solution since $-R_c$ and $-R_L$ on the one hand, and $+R_c$ and $+R_L$ on the other hand show similar concentrations of the different cations.

Discussion

Our results show that localizing the supply of H_2PO_4 , NO_3 , K or Ca generally results (a) in a lower total concentration of that nutrient in the shoot, but not always in the supplied root, and (b) in a stimulated rate of uptake by that root. The latter adds to the effect of compensatory root growth reported before (de Jager, 1982) accounting together for a rate of uptake per plant that is, after about 6 days, only slightly lower than that of the supplied control plant. The results also show the occurrence of redistribution of that nutrient to the non-supplied roots, though for the different nutrients to a very different degree.

It thus appears that for all these nutrients a lower concentration in the shoot coincides with a higher rate of uptake in the root. This indicates the existence of a control mechanism keeping concentration in the shoot near a set value. This may be effected through a negative feedback upon the rate of uptake in the root. This regula-

tory mechanism is suggested, for example, by Pitman (1972b) who observed that stimulation of relative growth rate (RGR) of the plant by increasing the light intensity, and thereby the nutrient demand of the plant, resulted in stimulated rate of uptake of K by the root (per unit root weight), and stimulated transfer to the shoot. Thus concentrations in the shoot were very little affected. A different kind of observation indicating internal control of the rate of uptake is the relative independence of rate of uptake from the concentration of the nutrient in solution (for P, Helder, 1951 and Asher & Loneragan, 1966). On the other hand the nutrient status of the plant strongly affects the rate of uptake as demonstrated e.g. by Leigh & Wyn Jones (1973) who compared the rate of uptake of ^{86}Rb and ^{22}Na by excised root segments of so-called low- and high-salt maize plants.

If a regulative system as suggested above exists, it must imply the transmission of information from shoot to root to adapt rate of uptake to shoot demand (Alberda, 1948; Ben Zioni et al., 1971; Lean et al., 1974). This information might have the nature of a hormone (1) or it might have a quantitative character and consist of sugars (2), the nutrient itself in one or another form (3) or a substance produced at assimilation of the nutrient in related amounts (4). It might also be that stimulation of the rate of uptake is a consequence of the stimulation of the rate of root growth as observed in our experiments (de Jager, 1982) (5). Here the information would be of an indirect nature.

To account for an assumed regulation of rate of uptake of NO_3 Ben Zioni et al. (1971) proposed a regulatory role for organic acid anions (sub 4), especially the malate ion. According to their hypothesis malate is produced in the shoot in amounts equivalent to nitrate, reduced, transported from shoot to root, and decarboxylated there upon arrival. The bicarbonate ion produced would then be exchanged for nitrate taken up, thus relating current nitrate reduction in the shoot, which depends on the N demand, and current nitrate uptake by the root. This scheme was more recently adapted by Kirkby & Knight (1977) to include nitrate reduction in the root and also other organic anions produced.

Since no specific exchange between bicarbonate and nitrate should be expected, this model would predict a general stimulation of the rate of uptake of all anions present in the nutrient solution. This is not in accordance with results that show a depressed rate of phosphate uptake when the rate of nitrate uptake is stimulated in response to a localized nitrate supply. The stimulation of the rate of K uptake that was observed here too can be considered as a secondary effect to maintain the cation/anion balance in uptake (de Jager, unpublished).

If the increased RGR of the root (de Jager, 1982), implying increased supply of carbohydrates, is accompanied by an increased energy status of the root (sub 2) then a stimulation of the rate of ion uptake might follow. An explanation of this kind has, among others, been given by Louwerse (1967) to explain the stimulation of nitrate uptake after a period of nitrate deprivation, producing so-called low-N/high-sugar plants. A possible explanation by the N level in the plant was here disregarded.

Increased RGR of the root also implies decreased average tissue age (sub 5). This might cause an increase in the rate of ion uptake if the rate of uptake is as-

sumed to depend much on root age in terms of days. This assumption might be true for Ca (Ferguson & Clarkson, 1975), but is questionable for K (Harrison-Murray & Clarkson, 1973), P (Ferguson & Clarkson, 1975) and Cl (Lauchli et al., 1978). In either way increased RGR of the root should stimulate the rate of uptake in an a-specific way and this is not in accordance with results of Hoffman (1968) who found a specific stimulation of K or P uptake after a period of K or P deprivation, nor with results of de Jager (1979) and de Jager & Posno (1979) who found a specific stimulation of P uptake after localizing the supply of P.

A possible role for hormones (sub 1) in the regulation of the rate of uptake can not be excluded and is in fact suggested by Pitman (1972b) and Pitman et al. (1974a, 1974b). They studied the influence of abscisic acid (ABA) on K uptake and observed a stimulation of the rate of uptake by ABA probably through a stimulation of the rate of transfer from root to shoot (xylem loading). ABA is known to be produced quickly in the shoot in response to water stress and it has been shown (Bous-siba et al., 1975) that also nutrient stress may stimulate the ABA level in certain plant parts. However, a specific stimulation by hormones of the rate of uptake of a nutrient does not seem to be obvious.

A more attractive hypothesis, therefore, would be that the nutrient itself functions as the messenger (sub 3), especially for those nutrients that are mobile in the phloem and that retain their ionic form in the plant completely (K and Cl) or partly (H_2PO_4). The concentration of these nutrients in the phloem sap, which probably is related quantitatively to their concentration in the leaf tissue (Geiger, 1975) might influence the concentration in the root and this in turn might influence the rate of uptake through negative feedback (Lean et al., 1974). Such a negative feedback is shown to exist in roots for NO_3 and Cl (Smith, 1973; Cram, 1973), and for K (Glass, 1975). Our data indeed show that a stimulated rate of uptake of K and NO_3 (Fig. 2) is correlated with a lower concentration of these ions in the root (K: Fig. 1; NO_3 : Table 2) and a similar correlation might exist for rate of uptake and internal concentration of H_2PO_4 (de Jager & Posno, 1979). Moreover, this negative correlation indicates that the primary effect of stimulated rate of uptake is not located in the outer absorbing cells (a 'push'), which would cause higher concentrations in the root, but somewhere in the inner root (a 'pull') (see Lauchli et al., 1971; Pitman, 1972a, on loading of the xylem).

The hypothetical system thus operates as follows. Starting from a complete nutrient supply, localizing the supply of, for example, H_2PO_4 to part of the root system causes a drop in shoot H_2PO_4 concentration. This causes lowered rate of H_2PO_4 loading of the phloem in the leaf, and unloading of the phloem in the root stele near to the xylem poles. Here the lowered H_2PO_4 concentration stimulates the process of xylem loading (pump two, Pitman, 1972a), draining H_2PO_4 from the surrounding tissues, steepening the gradient to the absorbing cortical and epidermal cells thereby lowering the concentration there. This then stimulates the rate of H_2PO_4 uptake (pump one, Pitman, 1972a), which is the observed phenomenon in our experiments. Since it is assumed that the activity of both pumps is regulated by negative feedback the term stimulation must be interpreted as derepression (see also Pitman, 1972a; Glass, 1975).

In a preceding paper (de Jager, 1982) it was suggested that the recovery of the RGR of the non-supplied roots in the treated plant would result from redistribution of the locally supplied nutrient resulting in a gradual increase of its sink strength. Although such a redistribution is shown to occur (Fig. 3) it may be questioned whether this is the only factor because redistribution only appears to result in a rise in concentration of the non-supplied roots when the experiments are started with plants that have a low concentration of that nutrient (H_2PO_4 and K in Fig. 1). Plants with a high concentration at the beginning of the experiments (NO_3 in Table 1, and N in Fig. 1) show a decrease in N concentration in the non-supplied roots and yet later the RGR of these roots is stimulated. However, if redistributed nutrient represents a more active fraction than the amount already present, then our explanation would still hold true despite decreasing total concentration. The relative magnitudes of redistribution of the different nutrients suits very well the observed differences in growth stimulation of the supplied root. The amount of redistributed N, for instance, is only 2.5 times the amount of redistributed P while the demand for N in tissues should be more than 10 times higher than the demand for P. So it is not surprising that the compensational growth of the supplied root is higher with N localization (de Jager, 1982), especially since the compensation in the rate of uptake is about the same for both nutrients (Fig. 2).

The occurrence of Ca redistribution as indicated by Fig. 3 is in accordance with results of Ringoet et al. (1968), van Goor & Wiersma (1974) and Wiersum (1979). Wiersum observed that the Ca concentration of the phloem sap, collected from *Ricinus*, was positively correlated with the Ca concentration in the leaves. It seems, therefore, not impossible that the uptake of even Ca is, at least partly, regulated by the flow of Ca descending through the phloem to the roots, although the amount of redistributed Ca is very small in comparison with the other tested nutrients, and not sufficient to maintain normal root growth at whatever rate (de Jager, 1982). Maybe, therefore, the increase in the rate of Ca uptake is also related, unlike that of the other nutrients, to the decrease in average age of root tissue, a hypothesis outlined already above.

The constancy of the total cation concentration (Table 2) may be considered from two points of view. Firstly, it indicates that uptake and assimilation of anions does not depend in a direct way on K nutrition and is related more to plant demand as modified by a limiting factor such as K nutrition. Secondly, within the group of cations one ion may replace the other easily although in a different way in shoot and root. In the shoot of the non-supplied plant ($-S_L$) it is especially Mg, and only to a little extent Ca, that replaces K, while Na is clearly depressed. In the roots of non-supplied plants ($-S_R$) Mg and Ca are stimulated in the same way, but Na is stimulated also. Clearly K deficiency leads to lower Na transport to the shoot, perhaps by a higher activity of the pump that loads K and Na into the vacuole. Bange & van Vliet (1961) propose that only Na that leaks from the vacuole can reach the xylem and a higher activity of the inwardly directed vacuole pump, which by negative feedback may follow from K deficiency, will decrease leakage and subsequent transport to the shoot. In the treated plant the picture is more complex. On the one hand K concentration in the shoot ($+S_L$) is almost normal but on the other Mg is

stimulated and Ca and Na are somewhat depressed. This change in favour of the Mg concentration is likely to follow from the fact that K-deficient ($-R_L$) and K-rich roots ($+R_L$) are attached to the same plant.

As commonly observed (Brouwer, 1962), the shoot-root ratio in the non-supplied plants decreased steadily. Fig. 3 shows that this is accompanied by a slight increase in content of the roots of the deficient nutrient. This net flux to the roots, if real, could be the cause of the relative, and sometimes absolute, stimulation of root growth. A possible explanation may be that during transport in the xylem nutrients are more readily absorbed by surrounding tissues (see Sutcliffe, 1975; van Bel, 1978) than in the phloem, so that a mobile circulating substance would tend to be accumulated in the root. Anyway the fact that in these non-supplied plants the limiting factor for root growth, the deficient nutrient, is coming from the shoot conflicts with the generalization that organs that are nearest to a limiting source will suffer least from this limitation (Brouwer, 1962). It agrees, however, with a later conclusion of Brouwer (1984) that at nutrient deficiency the composition of the phloem content gets less adequate for leaf growth than for root growth.

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