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Effects of localized supply of H_2PO_4, NO_3, SO_4, Ca and K on the production and distribution of dry matter in young maize plants

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Summary

The effect of localized supply of H_2PO_4, NO_3, SO_4, Ca and K on (net) production and distribution of dry matter was studied in young plants of *Zea mays* L. with four crown roots.

Roots of treated plants were divided between two compartments, one root receiving a complete nutrient solution (supplied root) and the other three a solution lacking one nutrient (non-supplied roots). In the control plants all roots received either a complete solution (+control) or a solution lacking one nutrient (−control).

Localizing the supply of a nutrient did not significantly affect the rate of dry matter production, nor the shoot/root ratio. The treatment, however, did cause a shift in the distribution of dry matter within the root system, in favour of the supplied root. Except for Ca, this effect was only temporary. The weight ratio supplied root/non-supplied root ($+R_1/-R_1$) after the period of adaption was highest for NO_3 and decreased in the order K, H_2PO_4, SO_4, whereas for Ca $+R_1/-R_1$ still rose at the end of the experiment. This ratio is mainly determined by growth stimulation of the supplied root, the duration of the period of stimulation being not much different.

Possible explanations for the differences in response are discussed in terms of (a) differences in demand of the roots that are dependent on internal supply and (b) differences in phloem mobility of the nutrient concerned.

Introduction

In soil an uneven distribution of a nutrient may easily occur, particularly in a vertical direction, as a consequence of fertilization, deposition of plant debris or

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the movement of water by gravitation or evaporation. Especially when the topsoil is not regularly homogenized – in natural habitats but also in the case of reduced cultivation (Russell, 1977) – phosphate and potassium will be concentrated in the upper layer of the topsoil (Drew & Saker, 1978b) whereas at the same time, at least in humid climates, nitrate may migrate downward. Apart from an uneven distribution, the availability of a nutrient may be restricted, for example in a drying top-soil, limiting the uptake by roots to the deeper layers of the soil. Therefore a plant will, in most cases, come across the bulk of a nutrient with only a part of the root system.

Field experiments comparing the effect of banded (i.e. locally supplied) with broadcast fertilizer application show that, to obtain the same yield of a certain crop, in the case of banding lower amounts of fertilizer are required. This holds especially for phosphate in soils that are low in (water-)soluble phosphate (Prummel, 1957).

Summarizing literature, de Wit (1953) developed a model to predict plant production in response to local addition (in a band) of P, N and K under different climatic conditions, based on the morphological and physiological responses in the root system.

Generally, the literature shows that localized supply of nutrients, especially of P and N, induces strong local reactions in the root system. These reactions concern stimulation of the rate of root growth and of the formation of laterals as well as stimulation of the rate of uptake at the site of application of the nutrient concerned (e.g. Goedewaagen, 1942; Drew et al., 1973; Drew, 1975; Drew & Saker, 1978a), or predominantly stimulation of the rate of uptake (Gile & Carrero, 1917; Lean et al., 1974; Frith & Nichols, 1975).

In this paper a comparison is made of the effects of localized supply of H_2PO_4, NO_3, SO_4, Ca and K on root growth with emphasis on the analysis of the time course of the reaction. Detailed knowledge of the latter may give a better insight into the mechanisms governing the growth response than experiments with only one final measurement. Data on the rate of uptake will be presented in a subsequent paper.

Materials and methods

Seeds of *Zea mays* L. cv. 535 were sown in sand. After five to seven days the seedlings were washed free from sand, the seminal roots were partly or completely removed and the plants were transferred to a complete nutrient solution or a solution lacking one nutrient. After three to four days the seeds with the remaining roots (if any) were removed, leaving crown roots of the first whorl with a length of about 5 cm. Experiments were started after another three to four days when the length of the roots was about 15 cm. From the moment of transfer to the nutrient solution until the end of the experiments plants were growing under the following conditions: 16 hours fluorescent light at 28 °C and a relative humidity (RH) of about 30 %, and 8 hours dark period at 24 °C and a RH of about 45 %. The light intensity, of about 30 W m^{-2}, was fairly constant over a

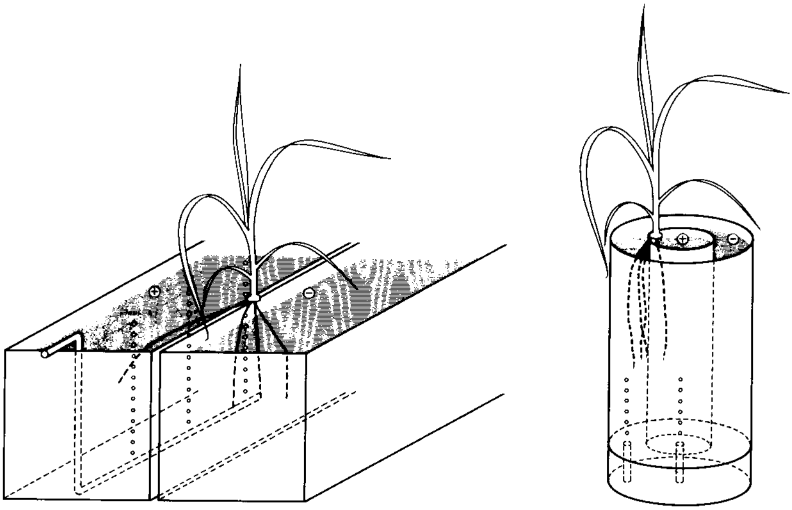


Fig. 1. Experimental set-up for dividing two parts of a root system between two compartments. In our experiments maize plants were grown with four crown roots of which one grew in a compartment containing a complete nutrient solution (+) and three in a compartment containing a solution from which one nutrient was omitted (–). The left arrangement consists of a number of rectangular containers, 15 cm × 15 cm × 120 cm, that are placed in paralel. The right container consists of two cylinders, one placed inside the other. The inner and the outer compartment contain about 1.0 and 3.5 litres, respectively.

Plants were fixed in holes in disks, laid over both arrangements. Solutions were aerated continuously.

distance of 10 to 60 cm from the source. In this range the plants were growing.

Deficient nutrient solutions were derived from the complete solution (after Steiner, 1968) by replacing the omitted ion as follows: K^+ by Ca^{2+}, Mg^{2+} and some Na^+; Ca^{2+} by Mg^{2+}; $H_2PO_4^-$ by SO_4^{2-}; SO_4^{2-} by Cl^-; NO_3 by SO_4^{2-} and Cl^-. The pH of fresh solutions was adjusted to 4.0 by the addition of diluted H_2SO_4. To prevent significant depletion, solutions were renewed frequently. In the meantime the pH showed a rise according to the size of the plants, necessitating a regular correction of the pH. The solutions were aerated continuously.

At the start of the experiments plants were mounted on sets of rectangular or circular containers in such a way that their roots were divided between two compartments (Fig. 1). Treated plants had one root in a complete solution and three in a solution lacking H_2PO_4, NO_3, SO_4, Ca or K. All roots of the control plants were placed in a complete nutrient solution (+control) or in a solution lacking one nutrient (–control). Plants from the treatment group and the control groups were arranged so that for each group light intensity was about equal. Plants were harvested systematically and not at random, to allow for the necessary thinning. At harvest the fresh weight of shoots and roots was determined, that of roots after rinsing for one minute with tap water followed by carefull blotting. After drying for 24 hours at 90 °C or at 70 °C (NO_3 variant), dry weight was determined and the material was stored for subsequent analysis.

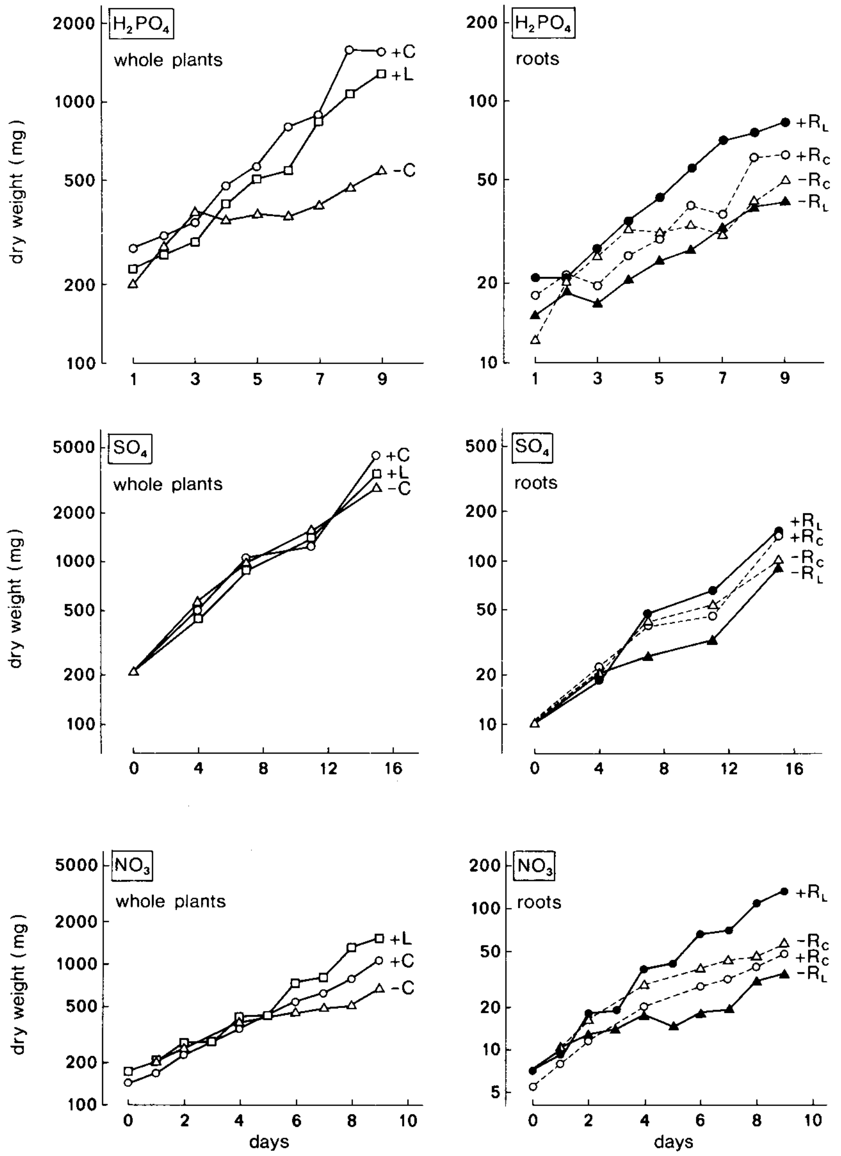
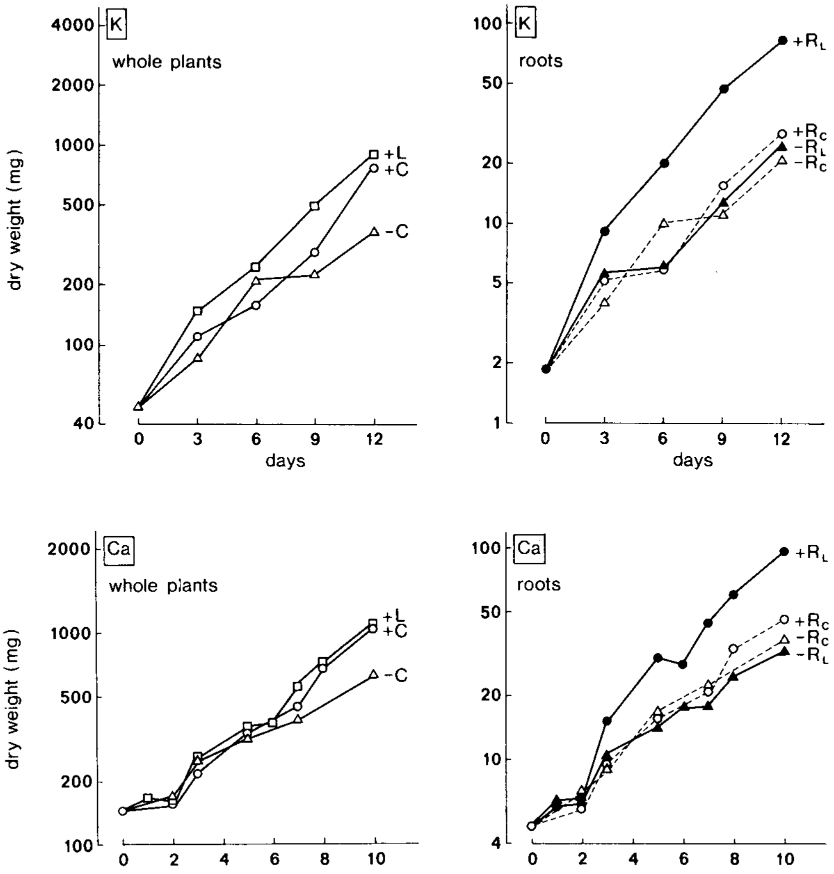


Fig. 2. The effect of localizing the supply of H_2PO_4, NO_3, SO_4, Ca and K, on the dry weight of the whole plant (left) and the single root (right). Since the weights have been plotted on a log-scale, the slope of the lines is equivalent to the relative growth rate (RGR). During pretreatment, the particular nutrient was either included (NO_3 and Ca) in, or excluded (H_2PO_4, SO_4, K) from, the solution.

Control plants (+ C and –C, symbols ○, and △) had all their roots in a complete nutrient solution (+ R_c, ○) or in a solution lacking one of the nutrients (–R_c, △). Treated plants (+ L, □) had one root in a complete nutrient solution (+ R_l, ●) and three in a solution lacking one of the nutrients (–R_l, ▲).



The number of replicates per experiment and per treatment is given in the following table:

	H_2PO_4	NO_3	SO_4	*Ca*	*K*
+C*, $+R_c$	4	3	4	7	4
+L, $+R_l$, $-R_l$	6	6	4	7	4
−C, $-R_c$	2	3	4	3	4

* For meaning of the symbols, see legend to Fig. 2.

Table 1. Shoot/root ratio (with standard deviation of the mean) in young maize plants of the treated plant (+L) and the control plants (+C and −C) at the end of the experimental period. In the treatment (+L) one nutrient was omitted from the solution of three out of four roots.

	H_2PO_4	NO_3	Ca	K	SO_4
+C	5.2 ± 0.2	4.8 ± 0.3	4.9 ± 0.7	6.0 ± 0.7	6.4
+L	5.0 ± 0.3	5.4 ± 0.3	4.6 ± 0.1	4.9 ± 0.7	7.0
−C	1.7 ± 0.1	2.0 ± 0.0	3.3 ± 0.3	3.4 ± 0.3	6.1

In the experiments concerning the localized supply of H_2PO_4, and of NO_3 the data for treated plants and for the control plants were collected in two subsequent experimental runs, which caused differences in weight at the start of the experiments.

Results

The effects of localizing the supply of H_2PO_4, NO_3, SO_4, Ca and K to one of the four roots on the growth of the whole plants are shown in Fig. 2 (left). Apparently the relative growth rate (RGR) of these plants (+L) is not affected by the treatment as compared with the plants with all roots supplied (+C). The plants uniformly supplied with a deficient solution (–C) show a reduced RGR within the experimental period except where SO_4 was omitted.

Dry matter distribution between shoots and roots in the +L plants does not differ significantly from that in the +C plants (table 1). In the –C plants the shoot/root ratio (S/R) decreased, except where SO_4 was omitted. This effect of nutrient deficiency on S/R was most pronounced for H_2PO_4 and NO_3.

Dry matter distribution between roots, however, was obviously influenced by the treatment. A comparison of RGR values of roots of +L and +C plants (Fig. 2, right), which is permitted because whole-plant RGR and S/R are not significantly different, shows that the supplied root of the treated plant ($+R_l$) has a higher RGR than a supplied root of the control plant ($+R_c$), whereas the RGR of a non-supplied root of the treated plant ($-R_l$) is reduced, even when compared with a root of the non-supplied control plant ($-R_c$).

This change in distribution of dry matter within the root system of the treated plant can be expressed by the $+R_l/-R_l$ ratio. Fig. 3 shows that after the beginning of the treatment this ratio rises during about six days and then becomes constant except in the case of Ca. A constant $+R_l/-R_l$ implies that both types of root have an equal RGR, that is, they acquire dry matter in the same proportion to their mass, which indicates a similarity in sink strength. Since the period of growth stimulation does not vary much, the differences in $+R_l/-R_l$ between the different nutrients, after the period of growth stimulation, is mainly determined by the degree of increase in RGR. This was highest for NO_3 and decreased in the order K, H_2PO_4, SO_4. For Ca the $+R_l/-R_l$ ratio was still increasing after 10 days.

A different result was obtained with localized K supply when low amounts of K were present in the solutions were K should have been absent. Fig. 3 (right hand, below) shows that the growth reaction in the roots is now much less pronounced. A similar effect may have occurred in the SO_4 experiment where also low amounts of SO_4 were present in the minus-SO_4 solution, which would offer a possible explanation for the absence of an effect on RGR and S/R in the –C plants. On the other hand, these plants showed clear symptoms of S deficiency, i.e. uniform yellowing of the younger leaves, so that this explanation is at least incomplete.

It must be borne in mind that the data given above cover a relatively short ex-

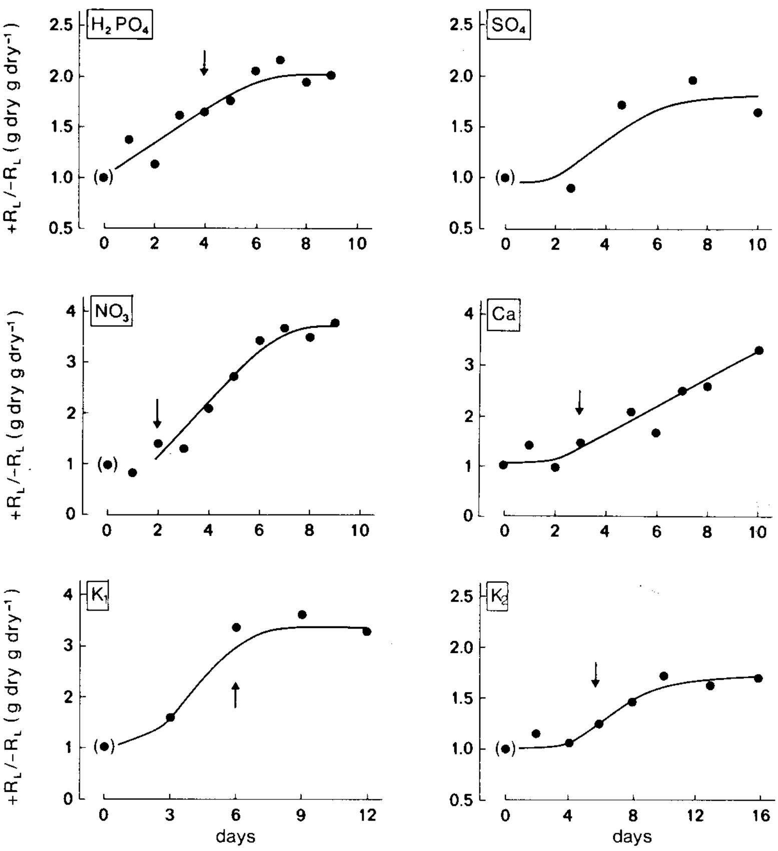


Fig. 3. The effect of localizing the supply of H_2PO_4, NO_3, SO_4, Ca and K on the distribution of dry matter within the root system as indicated by the ratio of the dry weight of the (one) supplied root ($+R_l$) to the mean of that of the (three) non-supplied roots ($-R_l$). Two experiments with localized supply of K are recorded here because of different results, probably due to a slight K contamination of the $-K$ solution in the second experiment (K_2). The arrow indicates the moment of the establishment of significantly differing dry weights of the $+R_l$ and the $-R_l$ (paired t-test, $P < 0.05$). For SO_4 no statistics could be applied.

perimental period (9 to 16 days) and apply to young plants in a period of exponential growth.

Morphological aspects

For all five nutrients the typical deficiency symptoms became visible within the experimental period.

The elongation rate of the root axis was generally checked by severe deficiency of N, P and K, while with Ca deficiency the root apex died. However, when the deficiency of P or N was less severe, the elongation rate of the root axis was stimulated. Such a stimulation may occur at an early stage of deficiency as a transient effect, and more or less as a steady state in non-supplied roots of the treated plant when the (P-)concentration around the supplied root is kept low (de Jager, unpublished). This accelerated rate of elongation at a low nutrient concentration in the environment is often (teleologically) called 'exploring type of growth' or 'seeking behaviour'. As a rule, in N- and P-deficient plants first-order laterals remain rather short and bear only few second-order laterals. In K- and S-deficient plants such data were not collected. In Ca-deficient roots ($-R_l$ as well as $-R_c$), the frequent dying of root tips even stimulated the formation of (brittle) laterals of which the tips also died within two days.

Discussion

Our results show that under the given circumstances and for the duration of the experiments, localizing the supply of H_2PO_4, NO_3, SO_4, Ca or K neither significantly affects the growth rate of the plant nor the shoot/root ratio, as compared with the +control plant. Yet the shoot/root ratio is considered a sensitive indicator of environmental changes (Brouwer, 1962 and 1963). However, the treatment substantially alters the distribution of dry matter within the root system in such a way that the supplied root shows an increased growth rate and the non-supplied roots a reduced one. Among all types of roots ($+R_c$, $+R_l$, $-R_c$, $-R_l$), the $+R_l$ shows the highest and the $-R_l$ the lowest RGR. After some time, however, the RGR of both parts of the root is equal again. The resulting enlargement of the supplied proportion of the root system from 25 % at the start of the experiment to a value ranging from 35 to 55 % depending on the nature of the nutrient, after about six days, partly compensates for the originally low uptake; changes in the rate of uptake are left out of consideration here.

Although most of the studies in the literature do not offer enough details to reveal the relation between the growth of the different parts of the root system with time, our results agree, in general, well with those of Goedewaagen, (1942), Miller & Ohlrogge (1958), Duncan & Ohlrogge (1959), Wilkinson & Ohlrogge (1962), Hackett (1968, 1972), McClure & Jackson (1968), Drew et al. (1973), Drew (1975), Drew & Saker (1978a), Coutts & Philipson (1977), and de Jager & Posno (1979). There seems to be less agreement with the results of Gile & Carrero (1917), Lean et al. (1974) and Frith & Nichols (1975), who observed no substantial growth reaction after localizing the supply of a number of nutrients. This may, in part, be a matter of methods since Gile & Carrero (1917) did not aerate the nutrient solutions and Frith & Nichols (1975) localized the supply of the complete nutrient solution, leaving part of the root system in deionized water.

Comparison of the morphology of the supplied roots of the treatment and the control reveals that in the case of P localization, the higher RGR of the $+R_l$ is essentially due to an increase in length of second-order laterals per cm of first-order lateral (de Jager, unpublished). Therefore, data on growth as increase in dry matter as well as on growth as lateral root formation are referred to above.

The effectiveness in influencing lateral root growth in different nutrients as observed by Wiersum (1958) decreased in the order NO_3, H_2PO_4, K, Ca and SO_4. This compares rather well with the effect of these nutrients on the $+R_1/-R_1$ ratio in our experiments, only the place of H_2PO_4 being different.

The extra growth of the supplied root at the expense of the growth of the remainder of the root system might be the consequence of a stimulated strength in the competition for carbohydrates of the root growing under the more favourable conditions. According to Wiersum (1958), the positive effect of a certain nutrient on the formation of laterals may be medaited by hormones (see also Drew et al., 1973, and Wilkinson & Ohlrogge, 1962) and effected through stimulation of the respiration. Indeed, in the supplied root, respiration may rise within two days from 30 to 70 % of the total ^{14}C influx into the root when one root of a minus-P plant is transferred to a P-containing solution. The same rise occurs in the non-supplied roots of that plant within five days (de Jager, unpublished). This observation agrees well with the known growth reaction and may indicate that the flow of carbohydrates through the phloem is driven by consumption at the sink, a view that is held by many authors, though the nature of the processes that govern transport form the phloem to the site of consumption is far from clear.

If indeed competition for carbohydrates regulates root growth, then the fact that after some time both parts of the root system of the treated plant show equal RGR values may be regarded as a recovery of sink strength of the non-supplied part. Since no such recovery seems to occur after localizing the supply of Ca, which is rather immobile in the phloem, the restored growth may very well result from internal translocation of the other nutrients to these roots.

Differences among these nutrients in the degree of growth stimulation of the supplied root after localizing the supply can, however, not be explained only by different mobilities in the plant, since the very mobile K and the mobile N produce a greater localization effect than does P, which is equally mobile (for a discussion of the respective mobilities see Pate, 1975). The greater effect of N and K must therefore be related to a greater demand of the non-supplied roots, defined as the amount necessary to maintain a normal concentration in newly formed tissue. So, despite similar mobilities in the plant, N imposes more restrictions on the growth of the tissues that depend on internal supply than does P, since the demand for N is at least ten times greater than that for P.

Brouwer & Loen (1962) infer from the results of their experiments that the N status of the shoot, depending on the number of roots supplying the shoot with N, if high enough, will permit normal growth of roots that are not supplied externally with N. Indeed, our results indicate that after a period of adaption 40 % of the root system can grow at a normal rate without an external supply of N. Still, according to Drew et al. (1973), the morphology of those roots might be somewhat different. These authors, and Stryker et al. (1974), in fact reject the possibility of sufficient internal transport.

A few authors report the absence of a growth response to localized supply of K (Lean et al., 1974; Drew, 1975). This is explained by its efficient circulation in the plant. Furthermore, according to Mott & Steward (1972), K may be needed in relatively small amounts and be irreplaceable only in the process of plasmatic growth. De Wit et al. (1963) estimate the critical level for K in plant material to be 0.2 meq per gram dry weight. On the other hand, according to Kirky & Knight (1977), considerable amounts of K may be bound by fixed organic anions in the leaf.

The effect of K in stimulating local root growth deserves further study since small amounts of K around the non-supplied roots may already obscure any effect (Drew, 1975; this article).

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