

# IONIC BALANCE AND GROWTH OF PLANTS

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CENTRUM VOOR LANDBOUWPUBLIKATIES EN LANDBOUWDOCUMENTATIE

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## 1 SUMMARY

Short time experiments with excised roots show that cations and anions from neutral salts are not necessarily taken up in equivalent amounts. Since electroneutrality must be maintained, any difference between both uptakes is balanced by exchange of  $\text{HCO}_3^-$  or  $\text{H}^+$ . Because of the concurrent change in the organic anion content the pH of the plant material remains around 6.

The total cation content  $C$  equals  $\text{K}^+ + \text{Na}^+ + \text{Ca}^{++} + \text{Mg}^{++}$ , and the total inorganic anion content  $A$  is  $\text{NO}_3^- + \text{H}_2\text{PO}_4^- + \text{SO}_4^{--} + \text{Cl}^-$ . The N and S in the organic form are present in the reduction stage of  $\text{NH}_3$  and  $\text{H}_2\text{S}$ . During reduction of  $\text{NO}_3^-$  and  $\text{SO}_4^{--}$ , the negative charge is released as  $\text{HCO}_3^-$ , which is either transformed into an organic anion or exchanged with an inorganic anion from the medium, or neutralised by  $\text{H}^+$  uptake. The ionic state of phosphate is not changed by its utilization.

The difference between the cation and inorganic anion content, the  $(C - A)$  content, is numerically equal to the organic anion content.

Ion selectivity and related competitive phenomena were mainly studied for plants growing on nutrient solutions with varying cation or anion composition. For cations, two competitive uptake systems are distinguished: a four-ion system concerning the ions K, Na, Mg and Ca, and a monovalent-ion system concerning K and Na. Both systems operate in Gramineous species, which differ from each other by their relative uptake of K and Na through the monovalent-ion system. The four-ion system is the only one operating in plantain, so that this species takes up the ions, K, Na, Ca and Mg competitively at about equal rates.

The anions  $\text{NO}_3^-$  and  $\text{Cl}^-$  appear to compete during the uptake by *Gramineae*.

The dependence of the  $(C - A)$  content on the composition of the nutrient medium was studied in experiments in which the nutrition is varied in such a way that the growth is not affected, but the anion and cation contents vary over a wide range. In these cases the plants appear to maintain their  $(C - A)$  content at a remarkably constant value. Depending on growing conditions other than the composition of the nutrient medium, this constant value is between 900 and 1100 me./kg for orchard grass and perennial rye-grass.

It is inferred that a constant  $(C - A)$  content is not due to the properties of the uptake and utilization mechanisms *per se* but to a regulation of its value during growth. The arguments are that the organic N content is considerably higher than 1000 gat./kg, the equivalency of the  $(C - A)$  content and the organic anion content is maintained throughout and that the  $(C - A)$  content is not constant in short time experiments. Regulation in the tops is only possible if sufficient organic anions and nitrates move upward as their salts and organic anions in excess of 1000 me./kg (for grasses) move again downward as their salts.

In small grains a stress on the (*C—A*) content develops when the availability of cations is low, the uptake of inorganic anions which stay as such in the plant is high and the reduction of nitrates in the shoots proceeds at a low rate. This stress on the (*C—A*) content is accompanied by a reduction of the growth rate.

A reduced growth rate with a normal (*C—A*) content may also occur, but a low (*C—A*) content is never accompanied by a normal growth rate. Hence, a normal (*C—A*) content is one of the conditions for a good growth.

Normal growth is possible at a wide variation of the *C* content, the *A* content and the contents of the individual ionic species, provided that the (*C—A*) content is normal. This indicates that the organic anions are essential for good growth. The cations are only necessary in amounts above 250 me./kg for K and 50 me./kg for Ca and Mg because they form neutral salts with the inorganic and organic anions. Among these cations the K ion plays a dominant role as a positive charge because it is readily taken up by most plant species. However, it can be replaced in this respect by Na, Ca and Mg when these are readily taken up.

An excessive *C* content or (*C—A*) content may occur in the case of K shortage in the presence of any other cation which is readily taken up. Although these other ions may function as a positive charge, the K ion seems to be the only one which accompanies the excess organic anions in their downward movement.

With ammonium fertilization growth proceeds often at a lower rate. This is due to a stress on the (*C—A*) content because of competition between  $\text{NH}_4^+$  and other cations and the release of  $\text{H}^+$  ions during the organic N formation.

A flow chart, summarizing the present knowledge with respect to the evaluation of the nutritional status of grass plants is given in figure 37. This flow chart can not be used for other species because they may differ in the relative uptake of cations (plantain) or in the normal (*C—A*) content (buckwheat, beets).

## 2 INTRODUCTION

In a review on the physiological basis for assessing the nutritional requirements of plants ULRICH (1952) showed that for the elements incorporated in the organic material, analyses of the plant for the anions  $\text{NO}_3^-$  (in case of nitrate supply),  $\text{SO}_4^{--}$  and  $\text{H}_2\text{PO}_4^-$  is more informative with respect to the nutrient status than analyses for total N, S and P. With sugar beets, nitrogen shortage is absent if the nitrate content of the petioles of recently matured leaves is higher than 75 me./kg<sup>1</sup>. DIJKSHOORN (1958), VAN BURGH (1962), DIJKSHOORN, LAMPE and VAN BURGH (1960) and DIJKSHOORN and LAMPE (1961) showed that the supply of N, S and P is sufficient for grass if the  $\text{NO}_3^-$ ,  $\text{SO}_4^{--}$  and  $\text{H}_2\text{PO}_4^-$  content is higher than about 100, 50 and 20 me./kg respectively.

A differentiation cannot be made for the cationic elements because they are not subject to distinct chemical transformations. With the elements K and Ca definite deficiency symptoms develop in small grains at contents lower than 200 and 50 me./kg, respectively (LUNDEGÅRDH, 1951). For Mg the level is also about 50 me. (BROESHART and VAN SCHOUWENBURG, 1961), and only traces of Na may be necessary. But plants may still respond to a supply with these elements when the contents are higher. Hence the diagnostic value of these limits is restricted.

Therefore, much attention has been paid to the contents of cations relative to each other, especially in view of the findings of VAN ITALLIE (1938, 1948) and BEAR (1950) on the constancy of the equivalent sum of the cations. They showed that in a rather remarkable number of cases the cation equivalent sum is a constant function of the cation composition of the nutrient medium, provided that the anion composition is not varied. With varying anion composition of the medium, the cation content may vary, but the ratio of cations and anions taken up was found to be around 0.8. This correlation between cation and anion uptake was connected with the maintenance of electroneutrality during uptake.

The work was expanded by SCHARRER and JUNG (1955, 1956), DIJKSHOORN (1957) and SAID (1959) who showed that the ratio of cation and anion uptake may decrease with increasing nitrate metabolism (table 10). It was assumed that the uptakes of cations and anions from neutral salts are directly coupled and that when the anion is nitrate, its transformation into the nonionic, organic form releases its negative charge internally as  $\text{HCO}_3^-$ , and that this  $\text{HCO}_3^-$  may exchange with another anion from the medium.

It will be shown in this paper that this assumption is at variance with results of short time experiments with, for instance, excised roots, and that the combined evidence

<sup>1</sup> All weights concern dry matter, unless otherwise stated.

obtained in other fields of research necessitates to assume that the organic anion content is regulated by growing plants. For this purpose short time experiments on the uptake and competitive interactions of cations and anions with excised roots are considered in sections 3 and 4. In section 5 experiments are discussed which, if based on the evidence of sections 3 and 4, should have resulted in a large variation of the organic anion content, but which invariably showed the absence of this variation and, therefore, rendered it necessary to assume that the organic anion content is subject to regulation.

Subsequently, the implications of this regulation with respect to the composition and the growth of plants are studied more in particular with respect to the agricultural aspects.

Speculations regarding the physiological mechanisms involved in the regulation observed proved to be unfruitful and are not included.

### 3 EFFECTS OF SALT SOLUTIONS ON THE IONIC CONTENTS OF PLANT MATERIAL

#### 3.1 SUMMARY

Evidence from literature is presented to show that the uptake rates of cations and anions may differ considerably depending on the salt used. The difference does not result in a change of pH of the plant material, but at any time and in any part of the plant the difference between cations and inorganic anions equals the organic anion content.

#### 3.2 SHORT TIME UPTAKE EXPERIMENTS

LUNDEGÅRDH and BURSTRÖM (1933) studied systematically the 10-hour uptake of cations and anions by young wheat plants from different neutral salt solutions at different carbon dioxide and oxygen pressures. The uptake of cations is plotted against the uptake of anions in figure 1. The observations show that cations and anions of neutral salts are taken up at unequal rates.

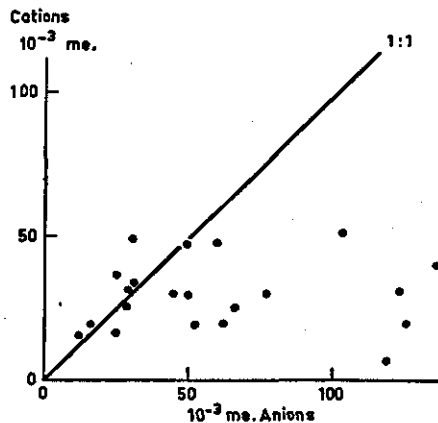


FIG. 1 The net uptake of cations and anions by 14 young wheat plants from 13 different salt solutions at various CO<sub>2</sub> and O<sub>2</sub> pressures of the air used for aerating during 10 hours. Data of LUNDEGÅRDH and BURSTRÖM (1933).

The uptake of cations and anions by excised roots of barley was studied also in detail by ULRICH (1941). His results are given in figure 2a. The uptake of the positive and negative ions from the neutral salts proceeds apparently with largely different



rates.  $K^+$  is taken up rapidly and  $Ca^{++}$  is taken up slowly, independently of the uptake rates of the anions such as  $SO_4^{--}$  and  $Br^-$ .

These observations agree with the concept of paired uptake only if excess cation uptake is balanced by the uptake of  $OH^-$  or  $HCO_3^-$  ions and excess anion uptake by the uptake of  $H^+$ . Another view is that the excess cation uptake is associated with the exchange of  $H^+$  and excess anion uptake with the exchange of  $OH^-$  or  $HCO_3^-$  ions. Experiments with labelled  $HCO_3^-$  ions in the solution were carried out (OVERSTREET, RUBEN and BROYER, 1940; JACOBSON, 1955 and HURD, 1956) to distinguish between both possibilities. But the interpretation of these experiments is difficult because the specific activity of the bicarbonate is likely to change owing to the relatively large amounts of bicarbonate associated with the living material and because the entrance of  $C^*$  is not indicative of the entrance of  $HCO_3^-$ . Obviously, there is no coupling between the cation and anion uptake from neutral salts and, at least in balance studies, the distinction between exchange with  $H^+$  or  $HCO_3^-$  and paired uptake with these ions is rather academic.

The amount of buffering compounds inside the plant material is small compared with changes in ionic contents due to salt treatments. Hence, if excess cations are taken up with  $HCO_3^-$  or exchanged against  $H^+$ , the internal pH must increase or the basic bicarbonate ion has to be transformed into the slightly basic carboxylate anion. The question of whether a difference between cation and anion uptake is accompanied by a change in internal pH or by a change in the carboxylate content is of course not academic and can be investigated.

ULRICH determined also the change in organic anion content in the barley roots used in the experiment of figure 2a. The difference between the uptake of the cation and the anion is plotted against the change in the organic anion content in figure 2b. Irrespective of the salt given, the cation minus anion uptake is practically equal to the change in the organic anions. Exceptions occurred with  $(NH_4)_2SO_4$  and  $Ca(NO_3)_2$ , probably because the N of  $NH_4^+$  and  $NO_3^-$  is incorporated into the organic material, so that changes in N content do not reflect changes in ionic content of the plant.

JACOBSON and ORDIN (1954) avoided any complication due to exchange and metabolism by not using nitrogen salts and by taking into account the exchange of ions not given as a salt. The ionic content of barley roots before and after treatment for three hours with four different solutions are given in figure 3a. The cation and anion contents changed markedly due to the treatments. In figure 3b the organic anion content of the roots is plotted against the cation minus inorganic anion content. Both changed because of the treatments, but to the same extent. Consequently, cations, balanced by  $HCO_3^-$  ions, are practically absent and there is no evidence of other ionic components present in amounts comparable to the cation, the inorganic anion and the organic anion content. The initial organic anion content of the barley roots was about 10 me./kg fresh weight and a three-hour treatment with  $KHCO_3$  doubled this content. Apparently, the rate at which the roots are able to form organic anions under the influence of a suitable salt treatment is large.

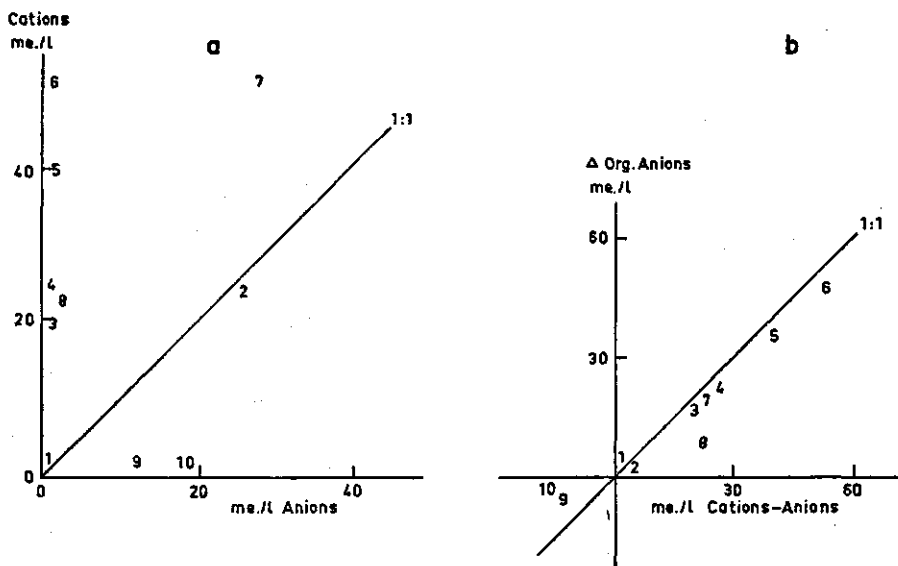


FIG. 2 a. The uptake of cations and anions by excised barley roots during 8 hours from ten different salts, as determined by changes in the solution. b. The change in organic anion content and the cation minus anion uptake, per liter of root sap. The numbers refer to: 1.  $\text{CaSO}_4$ ; 2.  $\text{KBr}$ ; 3.  $\text{K}_2\text{SO}_4$ ; 4.  $\text{KH}_2\text{PO}_4$ ; 5.  $\text{K-citrate}$ ; 6.  $\text{KHCO}_3$ ; 7.  $\text{KNO}_3$ ; 8.  $(\text{NH}_4)_2\text{SO}_4$ ; 9.  $\text{CaBr}_2$ ; 10.  $\text{Ca}(\text{NO}_3)_2$ . Data of ULRICH (1941).

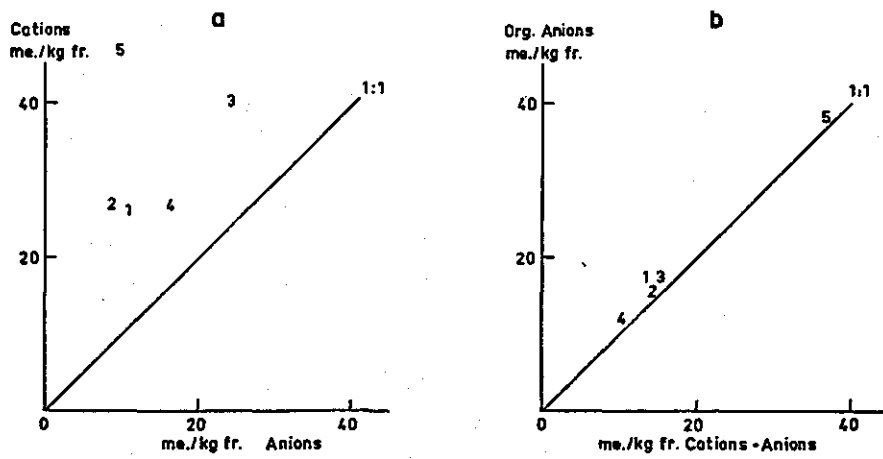


FIG. 3 a. The cation and anion content of barley roots before and after a three hour treatment with four solutions. b. The content of the organic anions and of the cations minus anions. The numbers refer to: 1. initial; 2. no salt; 3.  $\text{KBr}$ ; 4.  $\text{CaBr}_2$ ; 5.  $\text{KHCO}_3$ . Data of JACOBSON and ORDIN (1954).

From  $\text{CaBr}_2$  the  $\text{Ca}^{++}$  uptake was smaller than the  $\text{Br}^-$  uptake, and the organic anion content of the tissue correspondingly decreased during the treatment. The  $\text{Br}^-$  uptake was even higher from  $\text{KBr}$  than from  $\text{CaBr}_2$  and the  $\text{K}^+$  uptake was higher than the  $\text{Ca}^{++}$  uptake, which indicates association between cation and anion uptake. It seems that there is a limit to the excess of anion uptake rate over cation uptake rate because the organic anions available for breakdown in this process are present in restricted amounts and the plant material cannot maintain a process resulting in a marked drop of the internal pH (ULRICH, 1941).

An upper limit in the organic anion accumulation rate, and therefore in the excess cation uptake rate, is also probable. This upper limit may be reached when a salt with a readily accumulating cation and a slowly accumulating anion is given at a higher concentration. To test this the uptake from  $\text{Rb}_2\text{SO}_4$  and  $\text{RbCl}$  at concentrations of  $10^{-4}$  and  $10^{-2}$  eq./l by barley roots, was determined with a modified Epstein technique, as described by NOGGLE, DE WIT and FLEMING (1963). The results are given in table 1.

TABLE 1 Uptake rates in  $10^{-6}$  eq./l (140 min. g fresh) of the ions from  $\text{RbCl}$  and  $\text{Rb}_2\text{SO}_4$  by barley roots at concentrations of

	$10^{-4}$ eq./l			$10^{-2}$ eq./l		
	$\text{Rb}^+$	$\text{Cl}^-$	$\text{SO}_4^{--}$	$\text{Rb}^+$	$\text{Cl}^-$	$\text{SO}_4^{--}$
$\text{RbCl}$	6.9	4.6	—	23.0	18.7	—
$\text{RbSO}_4$	6.2	—	0.1	12.0	—	0.5

The  $\text{Rb}^+$  uptake rate at  $10^{-4}$  eq./l is the same from the  $\text{Cl}^-$  and the  $\text{SO}_4^{--}$  salt, although the  $\text{Cl}^-$  uptake is large and the  $\text{SO}_4^{--}$  uptake negligible. This proves again the absence of any direct relation between cation and anion uptake rate. At a concentration of  $10^{-2}$  eq./l the  $\text{SO}_4^{--}$  uptake is still negligible and the  $\text{Cl}^-$  uptake is large. But now the  $\text{Rb}^+$  uptake from  $\text{RbCl}$  is considerably higher than the  $\text{Rb}^+$  uptake from  $\text{Rb}_2\text{SO}_4$ . This association between cation and anion uptake at high concentrations may be due to a maximum excess cation uptake rate, originating from a maximum in the production rate of organic anions. Here, this maximum is about  $12 \cdot 10^{-6}$  eq./l (140 min. g fresh) which is in the same order of magnitude as the organic anion production rate under the influence of  $\text{KHCO}_3$  in the experiment of JACOBSON and ORDIN (figure 3).

The promoting effect of Ca salts on the  $\text{K}^+$  and  $\text{Rb}^+$  uptake is sometimes (BRIGGS, HOPE and ROBERTSON, 1961) ascribed to a possibly increased anion uptake caused by the addition of the anion with the Ca salt, although VIETS (1944) showed that it also occurs with addition of  $\text{CaSO}_4$ . NOGGLE, DE WIT and FLEMING (1963) observed a large increase in Rb uptake by barley roots while replacing  $\text{Rb}^+$  with  $\text{Ca}^{++}$ , keeping the  $\text{Cl}^-$  concentration the same (4.3.2). This shows that the promoting effect of Ca on the Rb uptake is not due to a coupling between cation and anion uptake.

### 3.3 IONIC CONTENT OF LEAF MATERIAL

The elements K, Na, Ca and Mg are predominantly in their ionic form inside the plant. Since minor elements and organic cations are quantitatively negligible, the total cation content of plant material is equal to  $C = K^+ + Na^+ + Ca^{++} + Mg^{++}$  equivalents. It will be shown in section 8.6 that the contribution of  $NH_4^+$  to the total cation content is small even when N is given as ammonium.

Phosphate is present either as the inorganic anion or in phosphorylated compounds. In both cases it corresponds with the ionic form of  $H_2PO_4^-$  (see also figure 4). The nitrogen is present either in the reduction stage of  $NH_3$  or as  $NO_3^-$ . It contributes only in the latter form to the inorganic anion content. Sulphate is present in the reduction stage of  $H_2S$  or in the inorganic form  $SO_4^{--}$ . The organic sulphur content of the protein of grasses, expressed in me.  $SO_4^{--}$ , is about 0.054 times the nitrogen content of the protein expressed in gramatoms (DIJKSHOORN, LAMPE and VAN BURGH, 1960). The  $SO_4^{--}$  content can therefore be calculated from the total S content by subtracting this calculated organic S content. Cl is in the inorganic  $Cl^-$  form in the plant. Therefore, the total inorganic anion content is equal to  $A = NO_3^- + H_2PO_4^- + SO_4^{--} + Cl^-$  me.

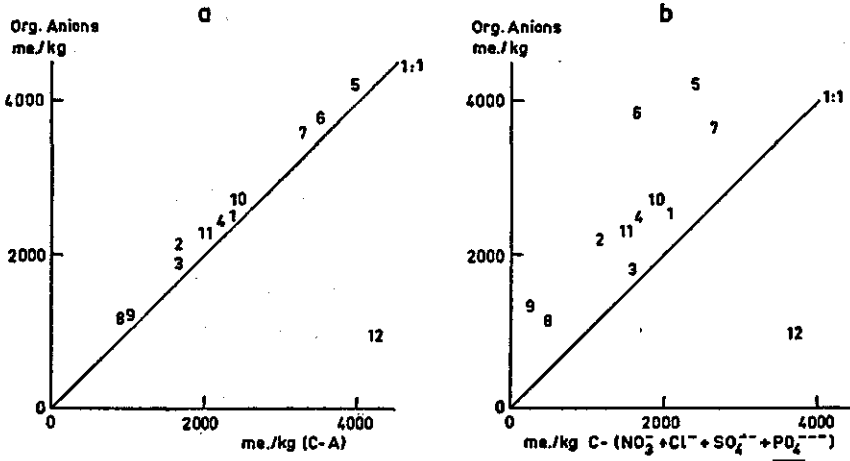


FIG. 4 a. The relation between the organic anion content and the (C—A) content of the leaves of 12 plant species. A is slightly over estimated because it includes total sulphur. Phosphate is included as  $H_2PO_4^-$ .

b. As figure a, but phosphate as  $PO_4^{---}$ . The (C—A) content and organic anion content are not at all equivalent when phosphate is included as  $PO_4^{---}$  or  $HPO_4^{--}$ .

The numbers refer to: 1. lima bean, 2. peas, 3. alfalfa, 4. soy bean, 5. beets, 6. spinach, 7. buckwheat, 8. blue grass, 9. wheat, 10. tomato, 11. lettuce, 12. cantaloupe (pH cell sap 7.5).

Data of PIERCE and APPLEMAN (1943).

PIERCE and APPLEMAN (1943) determined the (C—A) content and the organic anion content of 12 plant species (figure 4a). The observations are closely against the 1 : 1

line, which indicates that, in leaves, the excess of cations is also balanced by organic anions. Only the (C—A) content of cantaloupe is considerably higher than the organic anion content, which was found to correspond with a higher value of the pH of the cell sap.

In figure 4b, the phosphate content is calculated as  $\text{PO}_4^{--}$ . The scattering of the observations is now considerable, which shows that phosphate should be expressed as monovalent.

DIJKSHOORN (1962) determined the organic anion content and (C—A) content of perennial rye-grass, grown as described later in this paper. He found a (C—A) content of 1100 me./kg and an organic anion content of 1000 me./kg. The excess alkalinity of  $1100 - 1000 = 100$  me./kg may represent other organic ions,  $\text{HCO}_3^-$ , or may reflect analytical errors.

### 3.4 CONCLUSIONS

In short time experiments there appears to be no relation between the uptake of cations and anions from neutral salts. Any difference between the uptake of cations and anions and any reductive assimilation of nitrate and sulphate is reflected in a corresponding change of the organic anions, and at any time in any part of the plant the difference between the cation and anion content is practically equal to the organic anion content.

It is often concluded from these short time experiments that for growing plants differences in cation and anion uptake and in reductive assimilation of ions, and therefore in the organic anion content can be easily induced by varying the supply of cations and anions (compare CARLES, 1960). It is not difficult to find experimental results (compare section 7) which may support this conclusion.

However, such conclusions are not consistent with the findings of BEAR (1950) and others on the constancy of the total cation content and of the cation-anion ratio in plants, indicating regulation that comes to the fore when growing plants are considered. Such a regulation is not necessarily absent in short time experiments with excised roots, but it manifests itself far more pronounced when intact plants, growing under normal conditions, are considered.

To study this regulation it is desirable first to determine to what extent different plant species may show preference for different ions and and this preference is modified by competitive phenomena.

## 4 COMPETITIVE PHENOMENA

### 4.1 SUMMARY

Some well-known mathematical models of competition are discussed and applied to uptake data for whole plants and excised roots. In this way it appears possible to discriminate between competitive and other interactions.

### 4.2 MODELS OF COMPETITION

The  $n$  equations

$$U_i = \frac{b_i E_i}{b_1 E_1 + b_2 E_2 + \dots + b_j E_j + \dots + b_n E_n + 1} M_i^{(\infty)} \quad (1)$$

with  $j = 1, 2, 3, \dots, i, \dots, n$  and with proper designations for the symbols are widely used to describe competitive phenomena in physical and chemical engineering, physical chemistry, plant ecology (DE WIT, 1960) and animal ecology (VOLTERRA, 1928).

EPSTEIN and HAGEN (1952); FRIED and NOGGLE (1958); SCHUFFELEN (1954) and others used these equations to evaluate whether two ions affect each other competitively during the uptake by excised roots. In this case  $E_1, E_2, \dots, E_n$  represent the concentrations of ions of the same sign in the root medium,  $U_i$  is the uptake of ionic species  $i$ ,  $M_i^{(\infty)}$  is the (extrapolated) value of  $U_i$  at infinite concentration of this ion only, and  $b_i$  is a constant. The constant 1 in the denominator reflects the dependence of the competitive phenomena on concentration.

A concentration series of ion species 1 is defined as  $E_1$  variable and  $E_2, \dots, E_j, \dots, E_n$  each constant.

A replacement series of the ion species 1 and 2 is defined as  $E_1 + E_2 = E_{1+2} =$  constant and  $E_3, \dots, E_j, \dots, E_n$  each constant, hence an experimental series where the total concentration of ions in the medium is the same but the ratio of two varies between treatments. They enable the study of competitive phenomena between ions of one sign of charge without varying the ions of the other sign of charge in the treatment solution.

The factor

$$1 + \sum_3^n b_j E_j$$

can be eliminated with advantage by the following rearrangement. The abbreviation  $D$  is used for

$$1 + \sum_3^n b_j E_j \text{ and } D \frac{E_1 + E_2}{E_{1+2}} (= D)$$

is substituted for this factor in equation (1). Then

$$\begin{aligned} U_1 &= \frac{b_1 E_1}{b_1 E_1 + b_2 E_2 + \frac{D}{E_{1+2}} (E_1 + E_2)} M_1^{(\infty)} = \\ &= \frac{\left(b_1 + \frac{D}{E_{1+2}}\right) E_1}{\left(b_1 + \frac{D}{E_{1+2}}\right) E_1 + \left(b_2 + \frac{D}{E_{1+2}}\right) E_2} \cdot \frac{b_1}{b_1 + \frac{D}{E_{1+2}}} M_1^{(\infty)} \end{aligned} \quad (2)$$

Now

$$M_1 = \frac{b_1}{b_1 + \frac{D}{E_{1+2}}} M_1^{(\infty)} \quad (3)$$

is the uptake of species 1 for  $E_1 = E_{1+2}$  and  $E_2 = 0$ . The constant

$$k_1 = \left(b_1 + \frac{D}{E_{1+2}}\right) \quad (4)$$

is called the crowding coefficient of ionic species (1). Equation (2) can now be re-written as

$$U_1 = \frac{k_1 E_1}{k_1 E_1 + k_2 E_2} M_1 = \frac{k_{12} E_1}{k_{12} E_1 + E_2} M_1 \quad (5)$$

for species 1 and

$$U_2 = \frac{k_2 E_2}{k_1 E_1 + k_2 E_2} M_2 = \frac{E_2}{k_{12} E_1 + E_2} M_2$$

for species 2.

Only the relative crowding coefficient

$$k_{12} = \frac{k_1}{k_2} \quad (6)$$

can be determined in a replacement series.

The relation between the concentration and the uptake for both ions is linear if the relative crowding coefficient is 1. This is the case when  $b_1 = b_2$  and, irrespective of the values of  $b$ , when  $E_{1+2}$  is small compared with  $D$ . When the relative crowding coefficient is not equal to 1, the relations between uptake and concentration for both ions are curved to the same extent but in opposite directions.

The relative uptake of two ions in a replacement series is given by

$$a_{12} = \frac{U_1/E_1}{U_2/E_2} = k_{12} \frac{M_1}{M_2} \quad (7)$$

and is a constant function of the ratio between the ionic species concerned.

The values of  $M_1$ ,  $M_2$  and  $k_{12}$  for a replacement series can also be calculated from

concentration series for both ions. Instead of using equation (3) it is convenient to express this equation for the concentration series directly into  $M_1$ ,  $k_1$  and  $E_{1+2}$ , the latter value being the maximum value of  $E_1$  in the concentration experiment. This results in

$$U_1 = \frac{k_1 E_1}{(k_1 - 1) E_1 + E_{1+2}} M_1 \quad (8)$$

This equation is obtained by substituting 1 for  $k_2$  and  $E_{1+2} - E_1$  for  $E_2$  in equation (5).

Finally, equation (5) is extended to a replacement series of  $n$  ions by the  $n$  equations

$$U_i = \frac{k_i E_i}{\sum_{j=1}^n k_j E_j} M_i \quad (9)$$

with  $E_1 + E_2 + \dots + E_i + \dots + E_n = \text{constant}$ .

DE WIT (1960) gives more mathematical details and shows that at this stage two models of competition have to be distinguished.

*Model 1.* The observations of a replacement series fit equations (5) and those of a concentration series equation (8) and the value of  $k_{12}$  in equation (5) can be calculated from the constants  $k_1$  and  $k_2$  in equation (8) with equation (6). Only in this case the data fit the original equations (1).

*Model 2.* The observations of a replacement series fit equation (5); those of a concentration series may or may not fit equation (8), but the value of  $k_{12}$  cannot be calculated from the constants  $k_1$  and  $k_2$  in equation (8). In this case the data do not fit the original equation (1).

In plant ecology and animal ecology (DE WIT, 1960) competition according to model 1 is exceptional, but competition according to model 2 is not unusual. In physical chemistry it often is not possible to test the validity of model 1 because concentration series cannot be realized. In these fields of study the term competition is not restricted to model 1.

In case of ion uptake studies by growing plants the cation uptake often depends in some way on the anion uptake. In such cases it is not possible to interpret concentration experiments as described. The term competition is here also not restricted to model 1 if there is some circumstantial evidence for using this term.

To clarify the use of these equations examples of models 1 and 2 are given. One of these examples is also used to prove that competition between monovalent and divalent ions occurs.

## 4.3 EXAMPLES

### 4.3.1 Growing plants

With growing plants there is interaction between the cation uptake and the anion uptake. Since a cation cannot be added to a nutrient solution without adding an



anion, complications due to this interaction of the ions cannot be avoided in concentration experiments. Hence, to study selectivity and competition only replacement series can be used.

The technique of replacement experiments will be discussed in 5.2. As an example the results of two replacement series are given here, which concern Na-K replacement with perennial rye-grass and orchard grass as performed by SAID (1959). The composition of the herbage is plotted against the initial concentration of the replaced ions in the treatment solution of figure 5a and b. The K and Na contents of the plants

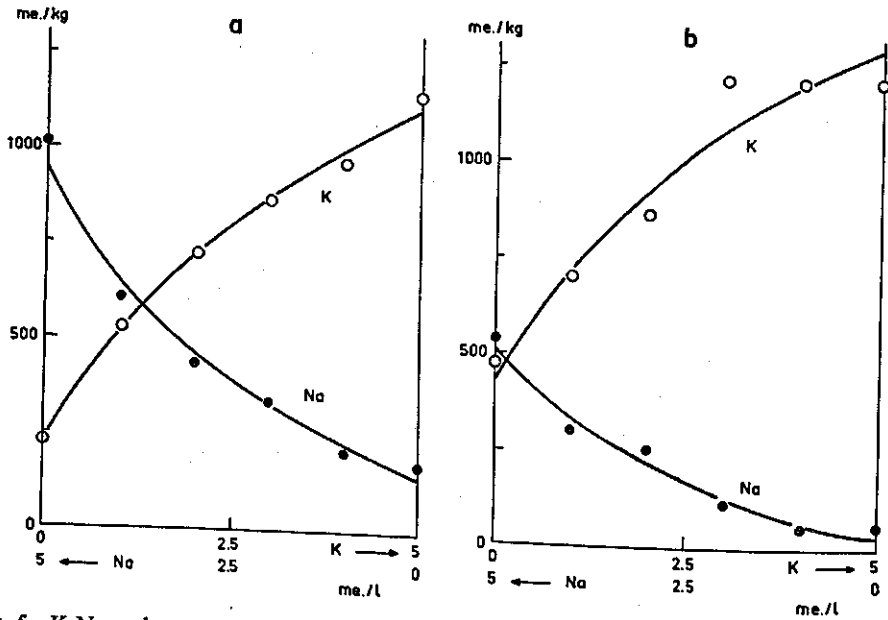


FIG. 5 K-Na replacement diagram for the herbage of perennial rye-grass (a) and orchard grass (b) grown in mixed culture. Initial composition of the solutions in me./l  
 K : x, Na : 5-x, Mg : 0, Ca : 0, NO<sub>3</sub> : 5, H<sub>2</sub>PO<sub>4</sub> : 0, SO<sub>4</sub> : 0, Cl : 0.  
 Period of regrowth on the treatments: 3 weeks  
 Renewal of solutions : 0 x  
 Average yield per container : 10 g  
 Data of SAID (1959).

grown without these elements in the treatment solution were not zero because these ions were introduced with the plant material. Contents at zero supply are called the K-load, the Na-load etc. The treatment differences did not affect the yield because of the presence of these loads, so that the differences between the contents at other treatments and the loads are the uptakes (*U*) of the ions concerned.

The K uptake line curves upward and the Na uptake line curves downward to the same extent. This indicates that a treatment according to equation (5) can be used. The curves as given in the graphs are obtained as described by DE WIT (1960). These lines represent equation (5) with the constants listed in table 2.

TABLE 2 Values of  $M$ ,  $k$  and  $\alpha$  for the curves in figure 5.

	perennial rye-grass	orchard grass	
$M_K$	880	860	me./kg
$M_{Na}$	800	490	me./kg
$k_{KNa}$	2.0	2.5	
$\alpha_{KNa}$	2.2	4.4	

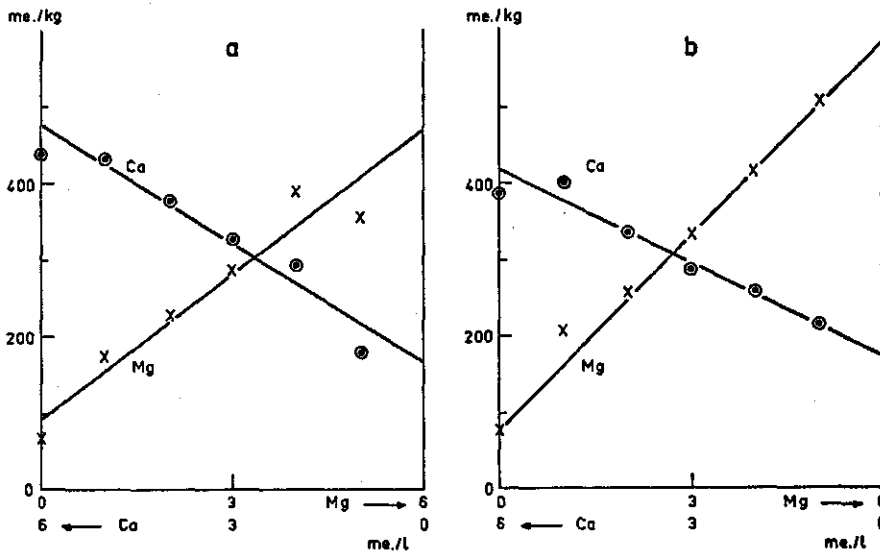


FIG. 6 Mg-Ca replacement diagram for the herbage of perennial rye-grass (a) and orchard grass (b), grown in mixed culture. Initial composition of the solutions in me./l  
Mg : x, Ca : 6-x, K : 1.5, Na : 0, NO<sub>3</sub> : 6, H<sub>2</sub>PO<sub>4</sub> : 0.5, SO<sub>4</sub> : 1, Cl : 0.  
Period of regrowth on treatments: 3 weeks  
Renewal of solutions : 0 x  
Average yield per container : 12 g  
Data of SAID (1959).

The relative uptake  $\alpha_{KNa}$  is calculated from the three other constants according to equation (7), and characterizes the difference between both grass species as far as the uptake of K and Na is concerned. This difference is mostly due to the difference in  $M_{Na}$ .

Since it is well known that monovalent ions may affect each other's uptake adversely in short time experiments with barley roots (EPSTEIN and HAGEN, 1952), the K-Na interaction is here an example of competition according to model 2. Because concentration experiments cannot be executed without introducing anion effects, it cannot be tested whether the two ions compete according to model 1.

The result of a Ca-Mg replacement series with both plant species is given in figure 6a and b (SAID, 1959). The observations are on straight lines so that the relative

crowding coefficient is 1 in both cases. The constants in equation (5) are given in table 3.

TABLE 3 Values of  $M$ ,  $k$  and  $\alpha$  for the curves in figure 6.

	perennial rye-grass	orchard grass	
$M_{Ca}$	310	220	me./kg
$M_{Mg}$	380	500	me./kg
$k_{CaMg}$	1	1	
$\alpha_{CaMg}$	0.82	0.44	

It may be that the Ca uptake and the Mg uptake are both proportional to concentration and independent of each other. Experiments with excised roots do not help much to distinguish between such a peaceful coexistence and competition with a relative crowding coefficient of 1 because in this case the uptake rates of divalent ions are small compared with the initial exchange reactions.

#### 4.3.2 Excised roots

There is very little relation between cation uptake and anion uptake by excised roots

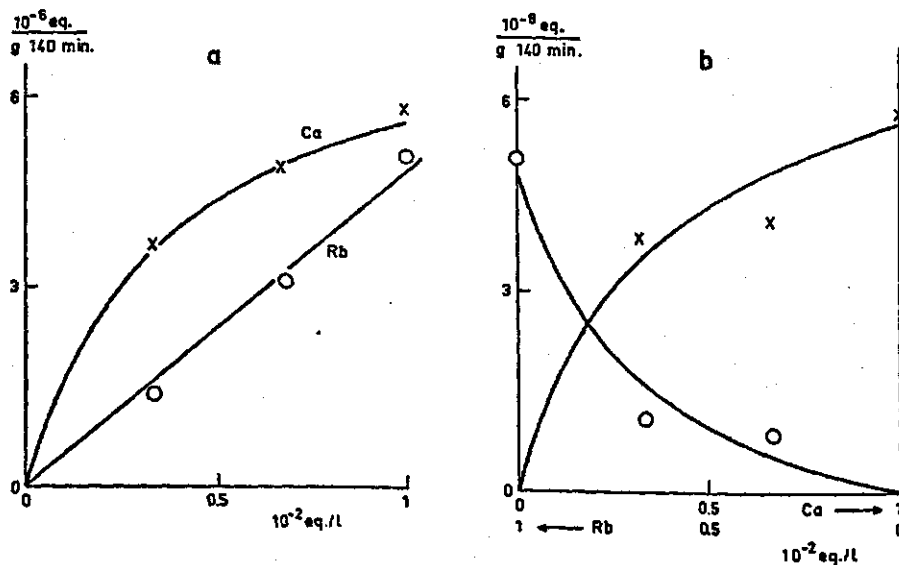


FIG. 7 Ca and Rb uptake rates by excised plantain roots from their chloride salts at concentrations around 10 me./l.

a. Concentration series. b. Replacement series.

The lines in figure b were calculated according to competition model 1 with the data in figure a. Data of NOGGLE, DE WIT and FLEMING (1963).

(3.2). Hence concentration experiments can be interpreted without paying undue attention to the other ion of the salt.

NOGGLE, DE WIT and FLEMING (1963) studied the interaction between Rb and Ca uptake of excised roots of barley and plantain (*Plantago lanceolata*). Two of the experiments will be discussed here to show an example of competition according to model 1 and of a much more complicated interaction.

The results of a Rb-Ca replacement series with plantain roots at a concentration level of  $10^{-2}$  eq./l of their chlorides are given in figure 7b. The Ca-line is bent upward and the Rb-line is bent downward. This indicates competition according to model 2. The results of two concentration experiments with these elements are given in figure 7a. These fit equation (8) with  $M_{Rb} = 4.8$ ,  $M_{Ca} = 6.5$  units,  $k_{Rb} = 1$  and  $k_{Ca} = 4$ . Hence the relative crowding coefficient  $k_{CaRb}$  in equation (5) is equal to  $4/1 = 4$ . The curves for the replacement series calculated with these constants are given in figure 7b and pass there through the observations. Apparently the data are not at variance with the supposition of competition according to model 1. But at concentrations around  $10^{-4}$  eq./l the two ions suppress each other's uptake also in some other way besides competition according to model 1 (NOGGLE, DE WIT and FLEMING, 1963).

One may question whether the basic equation 1 holds for a mixture of monovalents and divalents. But, even when the interrelations are governed by exchange reactions, the data have to be much more accurate and to extend over a wider range to find any effect of the valency not accounted for by the values of  $k$ .

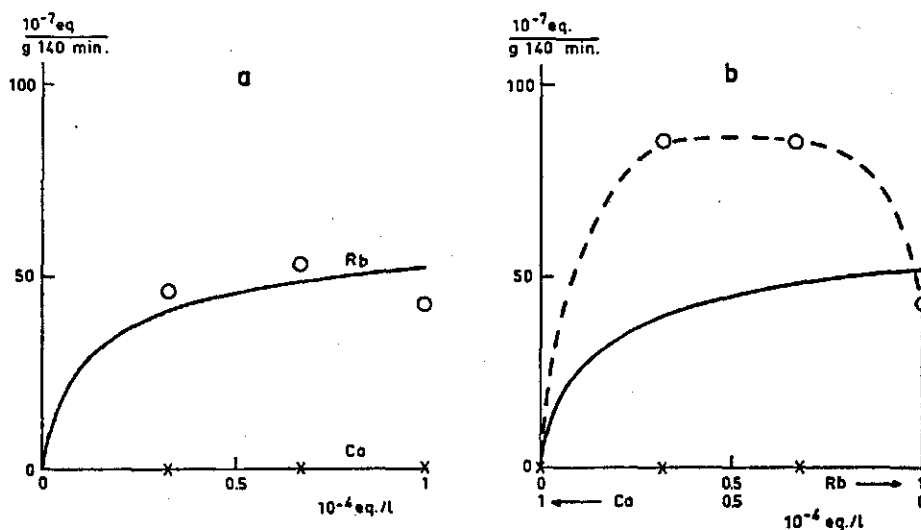


FIG. 8 Ca and Rb uptake rates by excised barley roots from their chloride salts at concentrations around  $10^{-1}$  me./l.

a. Concentration series. b. Replacement series.

The full drawn line in figure b was calculated according to competition model 1 with the data in figure a. Data of NOGGLE, DE WIT and FLEMING (1963).

The result of a similar experiment with barley roots at concentrations around  $10^{-4}$  eq./l is given in figure 8a and b. Based on the results of the concentration series we calculated the solid line in figure 8b for the replacement series. But the observations for Rb are on the dotted line, so that it is obvious that the interrelation is not competitive. The Rb uptake in the presence of Ca is even larger than in the absence of Ca in spite of the lower Rb concentration. This is known as the VIETS effect.

A further analysis (NOGGLE, DE WIT and FLEMING, 1963) showed that the Rb uptake rate in the absence of Ca cannot be maintained, but in the presence of Ca it behaves as other ions. Hence, this VIETS effect is of small importance for growing plants supplied with reasonable amounts of Ca.

The VIETS effect occurred also at concentrations around  $10^{-2}$  eq./l, although to a smaller extent. Here the Ca uptake was measurable and appeared to be depressed markedly by the presence of Rb, indicating some form of antagonistic effect between this monovalent and this divalent (figure 9).

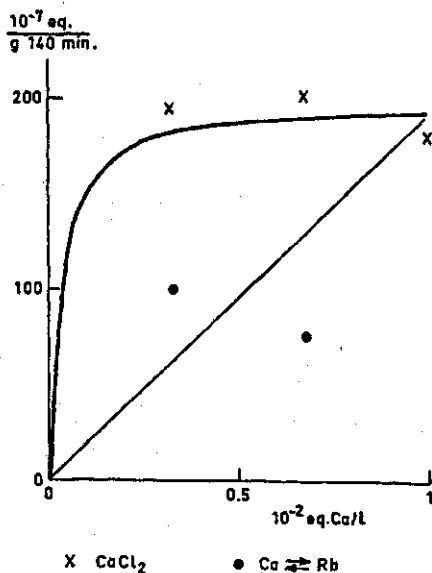


FIG. 9 The Ca uptake from  $\text{CaCl}_2$  at concentrations around 10 me./l in a concentration series and a replacement series with Rb. Data of NOGGLE, DE WIT and FLEMING (1963).

## 5 SELECTIVE ION UPTAKE BY GROWING PASTURE PLANTS

### 5.1 SUMMARY

The effect of varying cation or anion concentrations on the composition of the herbage is studied by means of an experimental technique developed by DIJKSHOORN (1956) and SAID (1959) and with the aid of the considerations presented in section 4.

It is shown that two competitive systems are operating for the cations. The four-ion system concerns K, Na, Mg and Ca and the monovalent-ion system K and Na. Both systems operate in grass, but in plantain only the four-ion system operates. The occurrence of competition between  $\text{NO}_3$  and Cl is also shown.

### 5.2 EXPERIMENTAL TECHNIQUE

Selectivity experiments with growing plants have been restricted to replacement series, to avoid interaction between cation and anion uptake. If in a nutrient solution one cation is replaced by another, the growth of the plants may be affected. This is likely to change the properties of the plant and to induce different degrees of exhaustion of the nutrient medium.

According to DIJKSHOORN a good growth rate, not affected by the composition of the treatment solution, is obtained when: (1) nitrate is supplied with the treatment solution, and (2) a reasonable supply of other elements is secured by starting an experiment with clipped plants and restricting the regrowth to some weeks.

The grass species orchard grass (*Dactylis glomerata*) and perennial rye-grass (*Lolium perenne*) and the dicotyledonous herb plantain (*Plantago lanceolata*) were used. The plants were taken from a normally fertilized field, the roots were cleaned and for each treatment plants mounted in perforations of  $30 \times 20$  cm covers of 6-liter containers. Subsequently the plants were clipped at 3 cm above the covers and transferred to the treatment solutions. Regrowth during two or three weeks took place in a greenhouse at 20–25 °C. No experiments were made during the winter.

During regrowth the transpired water was replenished by demineralized water. The regrowth, collected by clipping again at 3 cm, was dried, weighed and analysed. Sometimes the remaining plant parts were also harvested, the roots being rinsed in running tap water.

The dry weight of the starting material varied between experiments, but was the same for different replacement series of one experiment. The weight of the clipped plant material was about 40 g, that of the regrowth about 15 g and the total plant weight

at the end of the experiment was about 60 g. Within a series the yield did not vary systematically with treatments.

The treatments can be varied by renewing the treatment solutions 0×, 1×, 2× . . . during the period of regrowth. Experiments with some nutrient exhaustion appeared to give more information than experiments without exhaustion. Moreover, the practical value is obvious because plants in the field are also subject to exhaustion during growth.

In a series of experiments the sum of the four cations was kept the same, and one or more of the following replacement series were prepared:

$$E_k + E_{na} = \frac{1}{2} \Sigma E \quad E_{ca} = E_{mg} = \frac{1}{4} \Sigma E$$

and in the same way for K-Ca, K-Mg, Na-Mg, Na-Ca and Mg-Ca replacement series. The symbol  $\Sigma E$  represents the total initial cation concentration in me./l and the other symbols the initial concentrations of the ion species employed. Similar series were made for the anions  $\text{NO}_3^-$ ,  $\text{H}_2\text{PO}_4^-$ ,  $\text{Cl}^-$  and  $\text{SO}_4^{--}$ .

Treatments with one of the ions at zero supply were at first not used. When the disadvantage of this omittance became apparent they were included.

The treatment solutions were prepared by adding 1 N stock solutions to 6 liters of demineralized water. In the case of less soluble salts slight differences between the replacement series as to their anionic composition were introduced. Although this did not lead to any serious difficulties with the interpretations it would have been wiser to avoid this complication instead of some work.

The weights of the plant material were determined after drying at 105 °C, and the contents were determined with an error of about 5 per cent according to routine procedures used at the Institute in Wageningen. They are given in me./kg dry matter (N, P, Cl, K, Na as monovalents and S, Ca and Mg as divalents). Kjeldahl nitrogen includes only from 40 to 80 percent of the nitrate present and may have led to some underestimation of the total nitrogen content at contents above 2000 me./kg (DIJKSHOORN and LAMPE, 1960).

### 5.3 PLANTAIN

The cation content of the herbage of plantain grown on K-Na, K-Ca, Ca-Na and Ca-Mg replacement series is given in figure 10. The treatment solutions were renewed one time. The degree of exhaustion is not known because the whole plants were not analysed, but conductivity measurements indicated that it did not exceed 50 per cent before renewal of the solutions. The yield was a constant function of the treatment differences so that content minus load (content at zero supply of the cation) is the uptake by the herbage.

The cation contents are on approximately straight lines, so that the relative crowding coefficient in equation (5) is about 1 for all combinations. The values of  $M$  read in the graph are given in table 4.

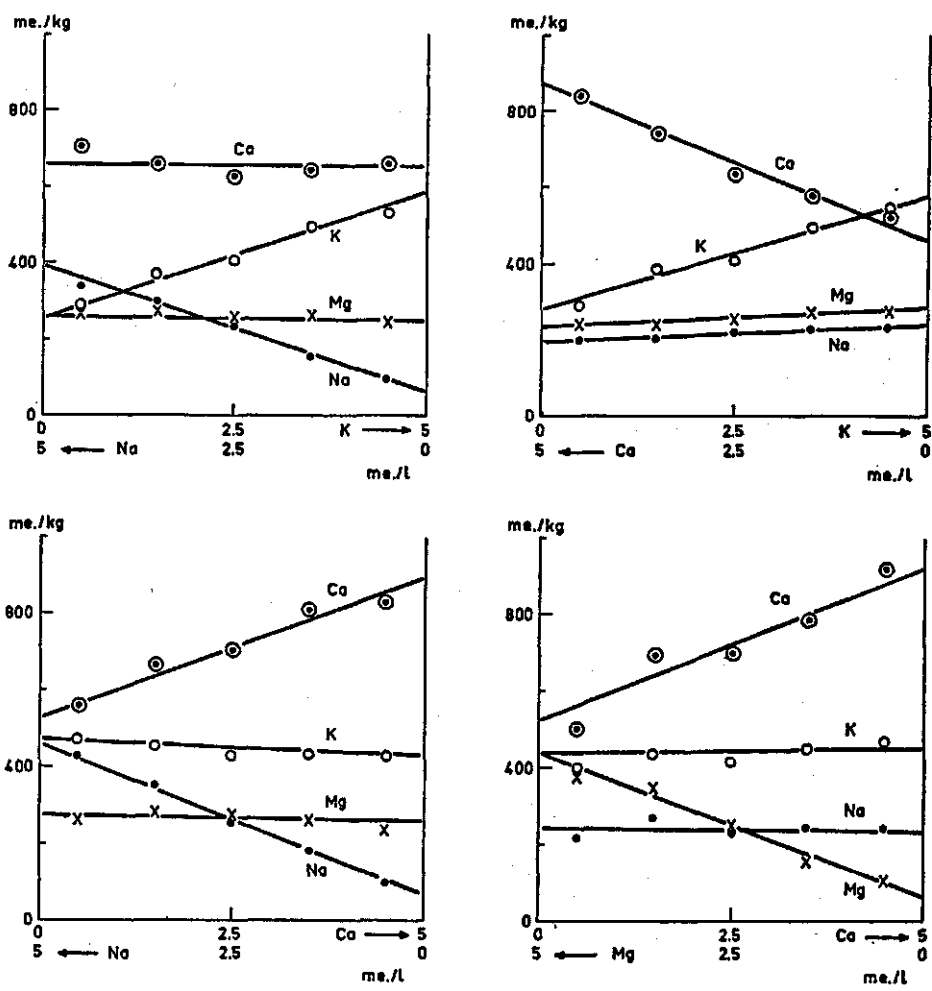


FIG. 10 Cation replacement diagrams for the herbage of plantain. Initial composition of the solutions in me./l

	Na-K	Ca-K	Na-Ca	Mg-Ca
K	x	x	2.5	2.5
Na	5-x	2.5	x	2.5
Mg	2.5	2.5	2.5	x
Ca	2.5	5-x	5-x	5-x
NO <sub>3</sub>	5	5	5	5
H <sub>2</sub> PO <sub>4</sub>	2.5	0.83	0.83	0.83
SO <sub>4</sub>	2.5	2.5	1.67	1.67
Cl	0	1.67	2.5	2.5

Period of growth on the treatments: 4 weeks  
 Renewal of solutions : 1 x  
 Average yield per container : 25 g



TABLE 4 Values of  $M$  for the curves in figure 10.

	K-Na	K-Ca	Ca-Na	Ca-Mg	average	
$M_{ca}$	—	410	375	405	395	me./kg
$M_{mg}$	—	—	—	370	370	me./kg
$M_k$	330	300	—	—	315	me./kg
$M_{na}$	325	—	390	—	360	me./kg

These values for any cation depend little, if any, on its partner ion in the replacement series. Therefore, they are averaged to estimate the relative uptake according to equation (7), with  $k = 1$ :  $\alpha_{cak} = 395/315 = 1.25$ ,  $\alpha_{mgk} = 370/315 = 1.18$ ,  $\alpha_{nak} = 360/315 = 1.14$ , and  $\alpha_{kk} = 315/315 = 1$ .

There is a slight preference in the order Ca, Mg, Na, K. It may be that either the ions compete equally well with each other or are taken up independently but in such a way that their uptakes are linear functions of their concentrations, which are the same for all four ions.

Since concentration experiments with growing plants cannot be interpreted easily, it is impossible to distinguish between these two processes on the basis of such experiments. But it was shown already that Rb and Ca ions compete with each other during the uptake by excised roots of plantain. Now it is very hard to imagine that with excised roots two ions compete, but are taken up independently of each other by growing plants.

If there were two systems of competition according to equation (5), for instance one for the combination K-Na and the other for the combination Ca-Mg, then the Mg and Na lines in the K-Ca replacement series would differ considerably from the horizontal, both in opposite directions (compare section 5.5). But since the lines are horizontal, it must be concluded that the four ions K, Na, Mg and Ca compete with each other according to the equations (9)

$$U_k = \frac{k_k E_k}{k_k E_k + k_{na} E_{na} + k_{mg} E_{mg} + k_{ca} E_{ca}} M_k$$

and so on, with about equal values for the crowding coefficient and for  $M$ .

#### 5.4 ORCHARD GRASS

The results of some replacement series with orchard grass are given in the figures 11 to 13. The experiments differ in the degree of exhaustion of the treatment solution, which was varied by the frequency of renewal. Roots and stubbles were also harvested in one experiment. The different response, compared with plantain, is evident from the K-Ca replacement series of figure 11. The K-line is curved, the Ca-line is straight and the Na content increases with decreasing K in the solution even with a constant supply of Na.

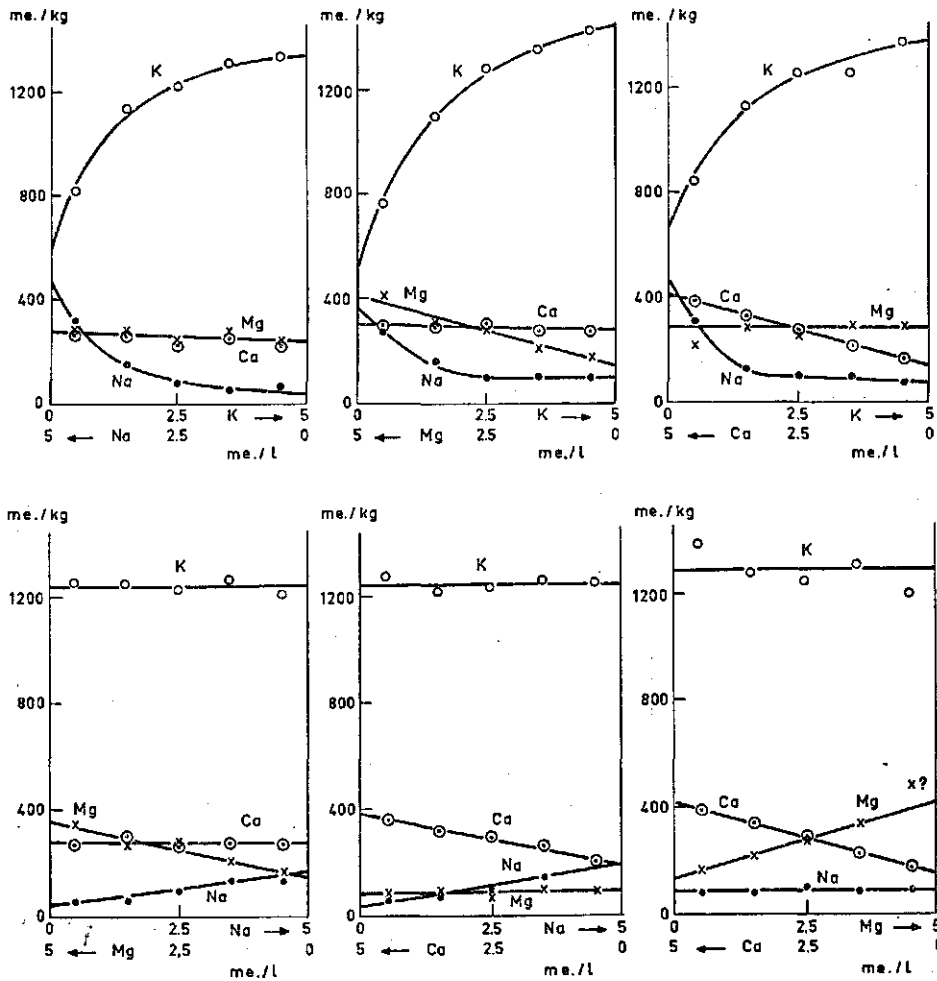


FIG. 11a Cation replacement diagrams for the herbage of orchard grass. Initial composition of the solutions in me./l

	Na-K	Mg-K	Ca-K	Mg-Na	Ca-Na	Ca-Mg
K	x	x	x	2.5	2.5	2.5
Na	5-x	2.5	2.5	x	x	2.5
Mg	2.5	5-x	2.5	5-x	0	x
Ca	2.5	2.5	5-x	2.5	5-x	5-x
NO <sub>3</sub>	5	5	5	5	5	5
H <sub>2</sub> PO <sub>4</sub>	2.5	0.83	0.83	0.83	0.83	0.83
SO <sub>4</sub>	2.5	1.67	2.5	1.67	1.67	1.67
Cl	0	2.5	1.67	2.5	0	2.5

Period of regrowth on the treatments: 17 days

Renewal of solutions : 2 x

Average yield per container : 17 g

In the Na-Ca series Mg was erroneously omitted.

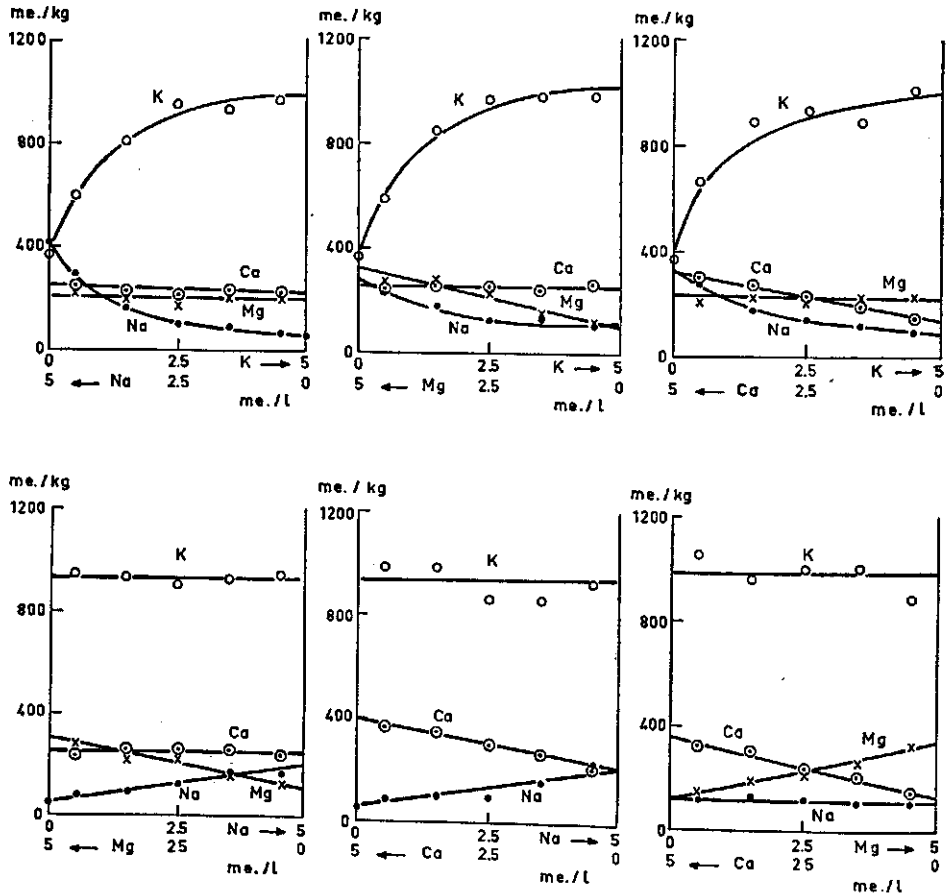


Fig. 11b Cation replacement diagrams for the whole plants of orchard grass, calculated from the dry weight and composition of the herbage (figure 11a) and of the roots plus stubbles. Average yield of whole plants per container: 46 g.

The increasing Na content with decreasing K content shows that these two ions effect each other in a competitive fashion, independent of the other cations given. This interaction was studied in detail by BANGE (1959) by means of short time experiments with corn seedlings. He found that the interaction between K and Na is governed by two competitive systems. In the first system K and Na are equally competitive, but in the second system the presence of K suppresses the uptake of Na rather effectively.

Figure 11 shows that, apart from where K is replaced, the relations between cation content and concentration in solution are very similar to those relations with plantain. This suggests that here also two competitive systems are operating. The first system is similar to that operating in plantain. The four ions K, Na, Ca and Mg are about equally competitive. The second system concerns the cations K, Na and probably H (5.4.2).

### 5.4.1 The four-ion system

The contents of the ions Na, Mg and Ca are linear functions of the concentration, except for the Na content in the replacement series with K (figure 11). Treated according to equation (5) the relative crowding coefficients are therefore about 1 and the uptake relations are then completely characterized by the values of  $M$ , given in table 5.

TABLE 5 Values of  $M$  for curves in figure 11.

	series					average	
	K-Mg	K-Ca	Na-Mg	Na-Ca	Mg-Ca		
HERBAGE (figure 11a)							
$M_{Ca}$	—	270	—	200	275	250	me./kg
$M_{Mg}$	270	—	215	—	285	250	me./kg
$M_{Na}$	—	—	130	155	—	140	me./kg
WHOLE PLANTS (figure 11b)							
$M_{Ca}$	—	180	—	190	220	195	me./kg
$M_{Mg}$	220	—	195	—	220	210	me./kg
$M_{Na}$	—	—	155	160	—	160	me./kg

It is evident that the values of  $M$  depend little on the partner ion in the replacement series. Therefore, they are averaged (table 6) to estimate the relative uptake according to equation (7) with an approximate value of 1 for the relative crowding coefficient.

TABLE 6 Relative uptakes calculated from the data of table 5.

	herbage (figure 11a)	whole plant (figure 11b)
$\alpha_{CaNa} =$	1.8	1.2
$\alpha_{MgNa} =$	1.8	1.3
$\alpha_{NaNa} =$	1	1
$\alpha_{KNa} =$	1	1 (estimate)

Because the uptake of K is mainly governed by the other system there is no similar way to calculate  $\alpha_{KNa}$ . The Ca and Mg lines in the replacement series with these ions at a constant concentration in solution are practically horizontal, in spite of varying K concentration and K content. The slope of the K curve at higher K concentrations is not larger than the slope of the Ca, Mg and Na lines in the replacement series with these ions. Since, moreover, BANGE (1959) proved with corn the existence of a system in which K and Na compete equally well with each other, it is reasonable to conclude that the relative uptake  $\alpha_{KNa}$  in this four-ion system is about 1.

With excised barley roots Rb suppresses the uptake of Ca (figure 9), which supports the supposition of competition between monovalents and divalents. Any competitive

effect of Ca on the Rb uptake with this material of course is overshadowed by the VIETS effect.

Taking into account all available information it must be concluded that the four ions, K, Na, Mg and Ca compete with each other according to equation (9)

$$U_{ca} = \frac{k_{ca}E_{ca}}{k_kE_k + k_{na}E_{na} + k_{mg}E_{mg} + k_{ca}E_{ca}} M_{ca}$$

and so on, with about equal values for the crowding coefficients and for  $M$ .

#### 5.4.2 The monovalent-ion system

Superimposed on the discussed four-ion system, a system for the K and Na uptake is present. The K-Na replacement series of figure 11 shows competition between both ions so that the results can be treated according to equation (5). For a correct procedure it is necessary to subtract first the uptake of these ions through the four-ion system. Since the uptakes through this latter system are relatively small and the accuracy of the data hardly warrants such a correction, all calculations are done on the data in the figure. The constants in equation (5) are given in table 7.

TABLE 7 Values of  $M$ ,  $k$  and  $\alpha$  for curves in figure 11.

	herbage (figure 11a)	whole plant (figure 11b)	
$M_k$	800	600	me./kg
$M_{na}$	460	370	me./kg
$k_{kna}$	6	6	
$\alpha_{kna}$	10	10	

The values of  $M_k$  and  $M_{na}$  are different for the herbage and the whole plant, but the values for the relative crowding coefficient and the relative uptake are the same for both. An analysis of the herbage gives here a good indication of the ion selectivity of the whole plant.

The Na uptake with no K in solution is considerably lower than the K uptake with no Na in solution. Since it has been shown that with barley roots the hydrogen ion competes at least with the uptake of the monovalent ions (FRIED and NOGGLE, 1958), this difference may be due to hydrogen ion competition.

If one thus supposes that in this monovalent ion system the (K + Na + H) uptake is independent of the K/Na ratio it is possible to transfer equation (9) into

$$\begin{aligned} U_k &= \frac{\alpha_{kk}E_k}{\alpha_{kk}E_k + \alpha_{nak}E_{na} + H} M_m \\ U_{na} &= \frac{\alpha_{nak}E_{na}}{\alpha_{kk}E_k + \alpha_{nak}E_{na} + H} M_m \\ U_h &= \frac{H}{\alpha_{kk}E_k + \alpha_{nak}E_{na} + H} M_m \end{aligned} \quad (10)$$

$U_h$  is defined as the apparent hydrogen ion uptake and is measured by the deficit in uptake of the neutral monovalents. The factor  $H$  characterizes the competition of the hydrogen ion and is constant possibly because the hydrogen ion concentration is a constant function of the treatments in the present experiment. The values of the constants  $M_m$  and  $H$  can of course directly be calculated from  $M_k$  and  $M_{Na}$  in table 7. They are for the herbage given in table 8.

TABLE 8 Values of  $M$ ,  $H$  and  $\alpha$  calculated from table 7.

$M_m$	860	me./kg
$H$	4	me./l
$\alpha_{kNa}$	10	

The value of  $H$  is in the same order as  $E_{Na}$  for  $E_k = 0$ , but much smaller than  $\alpha_{kNa} \cdot E_k$  for  $E_{Na} = 0$ . This means that the hydrogen ion competes effectively with the Na ion, but not with the K ion. This is the same in the experiment with orchard grass of figure 5 (4.3.1) as can be judged from the difference between  $M_k$  and  $M_{Na}$ . For perennial rye-grass this difference is small, indicating that around neutral pH the hydrogen ion competition with Na is also small. It will be shown later that in foxtail (*Alopecurus pratensis*) the competition of the hydrogen is small compared with K but large compared with Na. Apparently, grass species differ markedly in this respect.

In the experiment of figure 5 (4.3.1)  $\alpha_{kNa}$  was 4.4 and in the experiments of figure 11 it was 10. All calculations are based on initial concentrations; the treatment solutions were not renewed in the experiments of figure 5, but were renewed twice in the experiment of figure 11. The difference between the relative uptake in both experiments is probably caused by this difference in degree of exhaustion.

This is confirmed by a calculation of the exhaustion, which is possible on the basis of the data for the whole plants in figure 11b. The total supply of K in the treatments with 0.5 me.K/l was  $3 \times 6 \times 0.5 = 9$  me. K, the plant weight was 46 grams and the content was 380 at  $E_k = 0$  and 600 me. K/kg at  $E_k = 0.5$  me. K/l, so that the uptake was about 10 me. K. Hence at this supply, exhaustion was complete and the K content would have been higher if the supply had been increased by more frequent renewal. An experiment with practically daily renewal of the treatment solutions is given in figure 12. The relevant constants are given in table 9 together with those of the two other experiments.

TABLE 9 The effect of exhaustion on  $k$  and  $\alpha$ .

	figure				me./l
	5	11a (herbage)	12a	12b	
$E_k + E_{Na}$	5	5	5	3.3	
renewal sol.	0	2	12	12	
$k_{kNa}$	2.5	6	20	15	
$\alpha_{kNa}$	4.4	10	33	23	

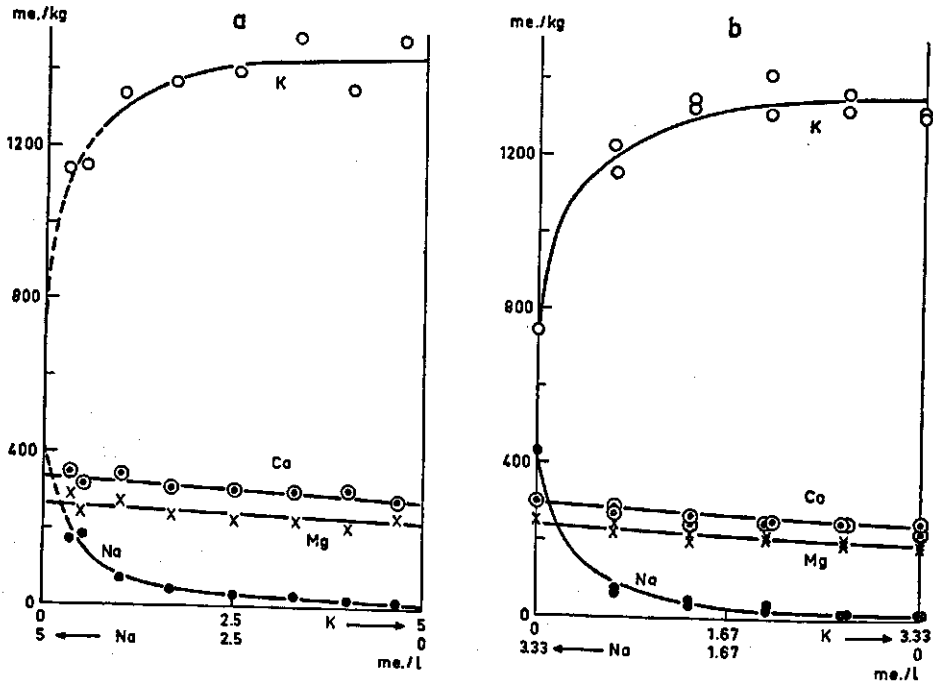


FIG. 12 K-Na replacement diagrams for the herbage of orchard grass. Initial composition of the solutions in me./l

	a	b
K	x	x
Na	5-x	3.33-x
Mg	2.5	1.67
Ca	2.5	0.17
NO <sub>3</sub>	5	3.33
H <sub>2</sub> PO <sub>4</sub>	2.5	0.17
SO <sub>4</sub>	2.5	1.67
Cl	0	0

Period of regrowth on the treatments: 18 days

Renewal of solutions : 12 x

Average yield per container a : 12 g

b : 12 g

The values of  $k_{KNa}$  and  $\alpha_{KNa}$  increase rapidly with decreasing degree of exhaustion so that without any exhaustion  $\alpha_{KNa}$  must be at least 50. This means that even with 0.05 me. K/l and 5 me. Na/l the K/Na ratio of the uptake through this monovalent ion system is still about 0.5. Hence Na uptake through this system proceeds only if the K supply is practically exhausted. The Na in plants grown without exhaustion of K is mainly taken up through the unselective four-ion system.

Plants differ markedly with respect to this uptake system for monovalents. It is

absent in plantain to such a degree that it cannot be detected in replacement series with growing plants. The Na uptake is affected to a different extent by the  $H^+$  concentration with orchard grass, perennial rye-grass and foxtail. With corn the Na in the tops taken up through this system is negligible (compare WYBENGA, 1957) and data of SUTCLIFFE (1956, 1957) in figure 13 show that slices of potatoes and beet tissue also differ considerably in this respect.

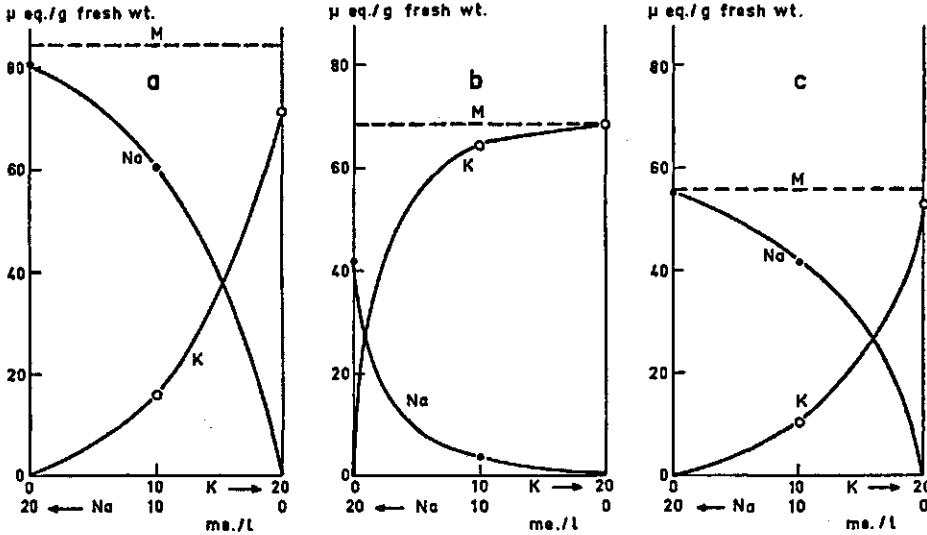


FIG. 13 K-Na replacement diagrams for washed beet disks (a), potato disks (b) and red beet disks (c) Composition of the solutions in me./l: K : x, Na : 20-x, Cl : 20. Period of uptake a: 2-40 hours; b: 2-70 hours; c: 2-12 hours. The solutions were renewed frequently enough to prevent severe exhaustion. Data of SUTCLIFFE (1956, 1957).

#### 5.4.3 Interaction between both systems

The rather independent operation of the four-ion and monovalent-ion system is particularly clear in the K-Ca and K-Mg replacement series of figure 11, where the Ca and Mg uptake lines are not affected by the widely varying uptakes through the monovalent ion system. It will be shown later that this does not hold where yield responses occur.

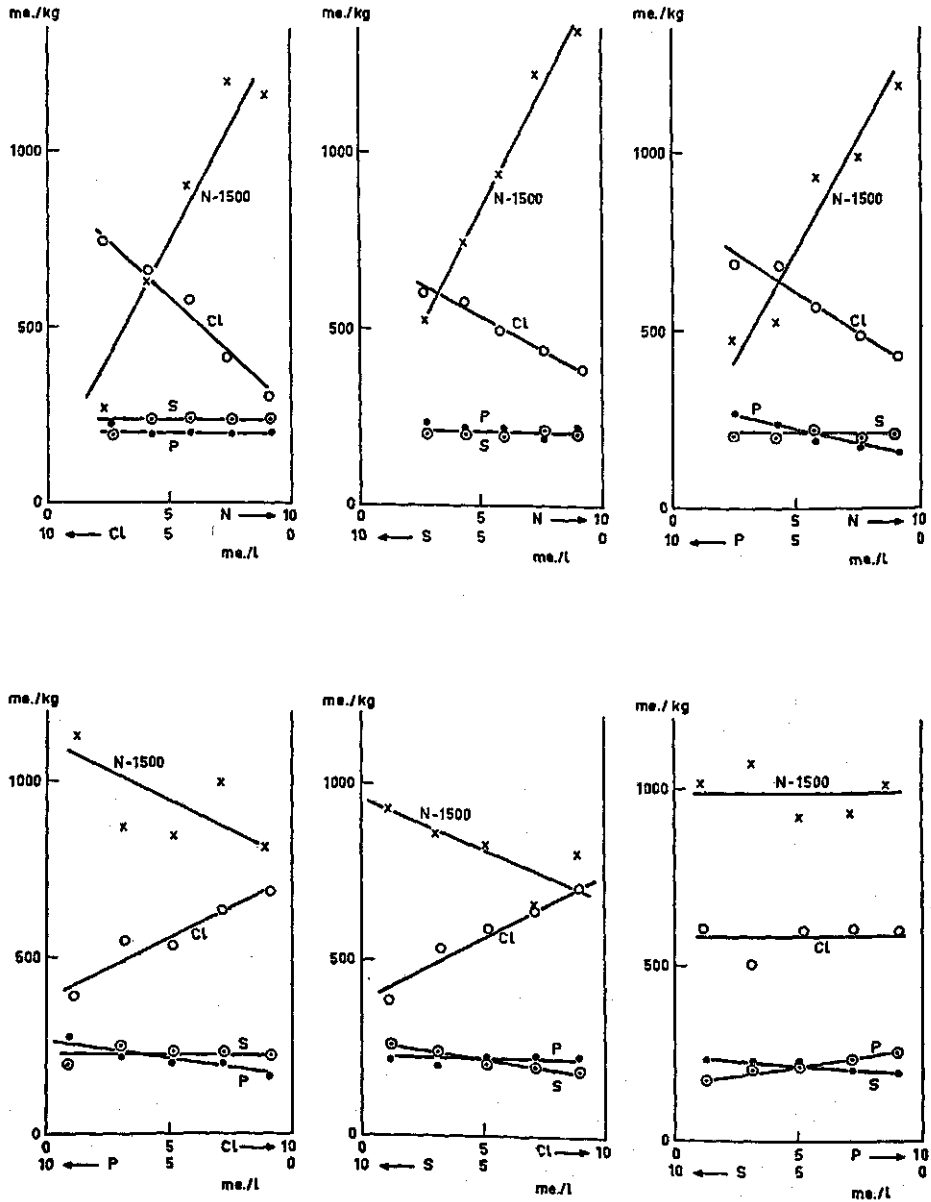
### 5.5 ANION UPTAKE BY PERENNIAL RYE-GRASS

An experiment with perennial rye-grass, incorporating all possible replacement series between  $NO_3^-$ ,  $H_2PO_4^-$ ,  $Cl^-$  and  $SO_4^{--}$  was carried out. Where  $NO_3^-$  is one of the replaced ions, particular care must be taken that the growth is not affected by N shortage. For this reason the smallest concentration of N used was 2.5 me./l. Further



details on the composition of the treatment solutions are given in the caption of figure 14.

The uptake of  $H_2PO_4$  and  $SO_4$  increases only slightly with the external concentration, within the range studied, but the  $NO_3$  uptake and Cl uptake increase considerably with increasing concentrations. Since the lines for both ions in the  $NO_3$ -Cl replacement series are about straight, any conclusion as to the competitive nature of the relation



cannot be made. But in the  $\text{NO}_3\text{-S}$  and the  $\text{NO}_3\text{-P}$  replacement series the Cl content decreases with increasing  $\text{NO}_3$  in solution, even though the supply of Cl is constant. A similar effect on the N-content is noted in the Cl-P and Cl-S replacement series. Here, the scattering may be due to incomplete recovery of the  $\text{NO}_3$  with the Kjeldahl modification used at that time, but the decrease in N content was also observed in other similar experiments. Some experiments, discussed later, show that the depressing effect on the N uptake manifests itself also in the  $\text{NO}_3$  content. Unfortunately, the samples of this experiment were discarded before the importance of an  $\text{NO}_3$  determination was realized.

The data suggest the existence of a competitive interaction between  $\text{NO}_3$  and Cl during the uptake by growing perennial rye-grass. This conclusion is supported by data of LUNDEGÅRDH (1959) on short time experiments with wheat plants. He showed that the  $\text{NO}_3$  and Cl ions in solution depress each other's uptake considerably.

FIG. 14 Anion replacement diagrams for the herbage of perennial rye-grass. Initial composition of the solution in me. per 6 liter

	Cl-N	S-N	P-N	P-Cl	S-Cl	S-P
$\text{NO}_3$	x	x	x	5	5	5
$\text{H}_2\text{PO}_4$	4	4	(10-x)	x	5	(10-x)
$\text{SO}_4$	4	(10-x)	4	5	x	x
Cl	(10-x)	4	4	(10-x)	(10-x)	5
K	15.5	15.5	15.5	10	10	10
Na	0	0	0	5	5	5
Mg	1	1	1	2.5	2.5	2.5
Ca	1.5	1.5	1.5	2.5	2.5	2.5

Period of regrowth on the treatments: 12 days

Renewal of solutions : 1 x

Average yield per container : 15 g

The N contents were brought within the scale of the graphs by subtracting 1500 me./kg; the scattering of the observations is absolutely correct but seems relatively too large.

## 6 REGULATION OF THE (C-A) CONTENT

### 6.1 SUMMARY

The effect of simultaneously varying the cation and anion supply on the ionic contents is studied under conditions where the yield does not vary appreciably with the treatments. Although there are large variations in the *C* and *A* contents, the (*C-A*) content appears to be a constant function of the nutrient supply. Depending on conditions, its constant value is found between 900 and 1100 me./kg for grasses. Taking into account the large variation of the organic anion content in excised roots following salt treatments, this indicates that growing plants can regulate their (*C-A*) content at a constant value (compare 3.4) at varying cation and anion uptake.

### 6.2 EXPERIMENTS

#### 6.2.1 Cation replacement

The anion and cation contents of the herbage grown on the K-Ca and K-Mg replacement series of figure 11 are given in figure 15.

The constancy of the *A* content over the greater part of the replacement range may

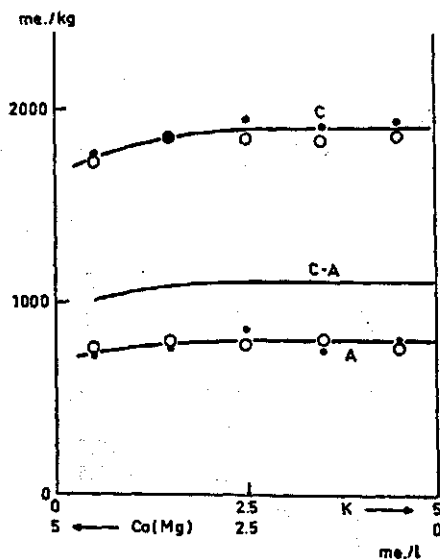


FIG. 15 The *C*, *A* and the (*C-A*) contents of the herbage grown on the K-Ca (o) and K-Mg (•) replacement series, presented in figure 11.

be readily related to the constancy of the anion supply, but it is not clear why the total cation content does not increase with the increase of the readily absorbed cation in solution. The reason may be either that the uptake rate of the cations is at its maximum as far as its absorption mechanism is concerned or that plants grow in such a way that the ( $C-A$ ) content is regulated at a constant value when cations are adequately supplied. The two possibilities may be distinguished by experiments with varying cation and anion supply.

### 6.2.2 Nitrate fertilization

SAID (1959) applied 0, 10, 20, 30 and 40 me. of K-, Na-, Mg- or Ca-nitrate to soil filled pots planted with perennial rye-grass or orchard grass. The cation status of the soil was such that the yields were not affected by the cation supply. Nitrate in the unfertilized pots was so high that the nitrogen fertilization increased the yield only by a little over 10%.

The fertilization affected the contents to a large extent as is illustrated in table 10 where contents at 0 me. and 40 me. nitrates per pot are given for both grass species.

The total cation content of both perennial rye-grass and orchard grass is practically independent of the cation given with the nitrate ion although the contents of the individual cations differ considerably. With both species the contents of ions taken up as cations and as anions increase with increasing nitrate fertilization. With perennial rye-grass, the uptake ratio of cations to anions decreases from about 0.65 to about 0.51 with increasing nitrate fertilization, but this ratio remains constant at about 0.60 with orchard grass (SAID, 1959). This difference between the grass species makes it difficult to generalize along lines of cation equivalent constancy and constancy of the uptake ratio of cations to anions.

Nitrate was determined and from organic N and total S the inorganic  $SO_4^{--}$  content can be calculated. Hence it is possible to calculate the inorganic anion content ( $A$ ) (2.3) and to relate this value to the total cation content ( $C$ ). This is shown for all treatments and both plant species in figure 16. The  $A$  content appears to vary from 600 to about 1100 me./kg and the  $C$  content from about 1600 to 2100 me./kg. The difference between the cation content and anion content is constant at 1000 me./kg for both species, throughout the whole range. This constancy is strikingly different from the results with excised roots as shown in figure 3, and it indicates that growing plants regulate the ( $C-A$ ) content within a rather narrow range, where possible. This range is the same for orchard grass and perennial rye-grass, even though there is a difference between the uptake ratio of cations to anions for both species. The organic N content without nitrogen fertilization is 1850 and with nitrogen fertilization 2200-2600 me./kg. The internal  $HCO_3^-$  production due the metabolic reduction of nitrate was, therefore, about 1850 and 2400 me./kg, but the ( $C-A$ ) content is in both cases about 1000 me./kg, which indicates that the organic anion content is not directly dependent on the nitrate metabolism.

TABLE 10 Elements in perennial rye-grass and orchard grass for some treatments of SAID (1959) (N monovalent, P monovalent). The  $\text{NO}_3$  content is the content of N present in this form inside the plant.

treatment	me./kg dry matter										elements taken up as		uptake ratio of cations to anions
	K	Na	Mg	Ca	Cl	P	S	organic N	$\text{NO}_3$	cations	anions		
PERENNIAL RYE-GRASS													
0	1030	140	185	345	340	105	240	1860	50	1700	2595	0.65	
40 me. $\text{KNO}_3$	1240	85	180	325	290	85	250	2490	420	1830	3535	0.52	
40 me. $\text{NaNO}_3$	690	740	200	310	235	95	240	2540	450	1940	3560	0.52	
40 me. $\text{Mg}(\text{NO}_3)_2$	895	195	335	415	280	90	215	2570	380	1840	3535	0.51	
40 me. $\text{Ca}(\text{NO}_3)_2$	860	180	235	495	245	70	195	2570	470	1770	3550	0.51	
ORCHARD GRASS													
0	1005	50	250	330	290	90	210	1900	120	1635	2610	0.63	
40 me. $\text{KNO}_3$	1530	25	265	325	270	80	180	2320	670	2145	3520	0.59	
40 me. $\text{NaNO}_3$	880	530	265	270	240	85	180	2300	630	1945	3435	0.57	
40 me. $\text{Mg}(\text{NO}_3)_2$	1020	140	465	370	260	75	185	2300	495	1995	3315	0.60	
40 me. $\text{Ca}(\text{NO}_3)_2$	970	145	355	450	245	75	180	2210	510	1920	3220	0.60	

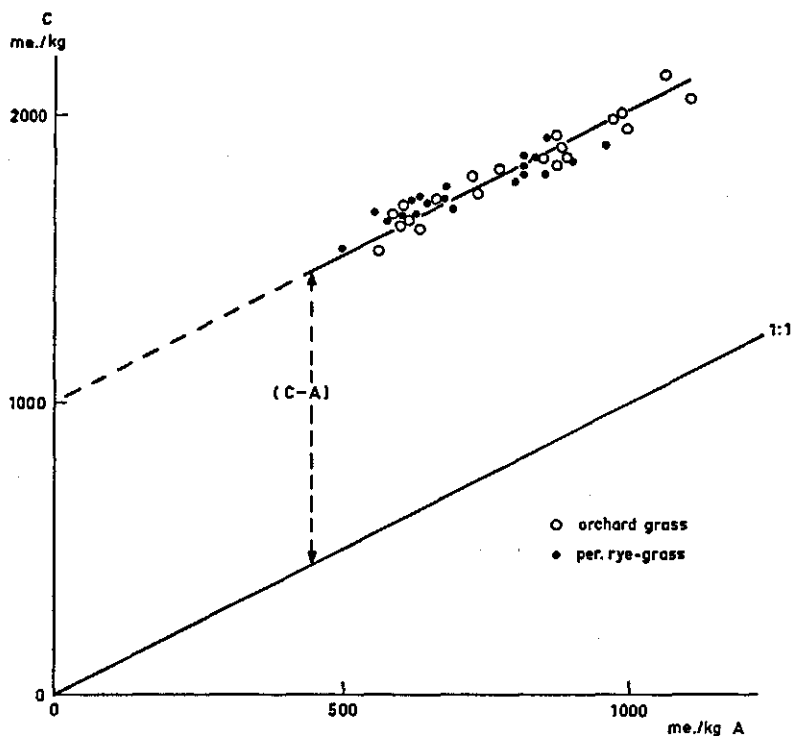


FIG. 16 The C and A contents of the herbage of orchard grass and of perennial rye-grass fertilized with 0, 10, 20, 30 or 40 me. nitrate as the K, Na, Mg or Ca salt. From data of SAID (1959).

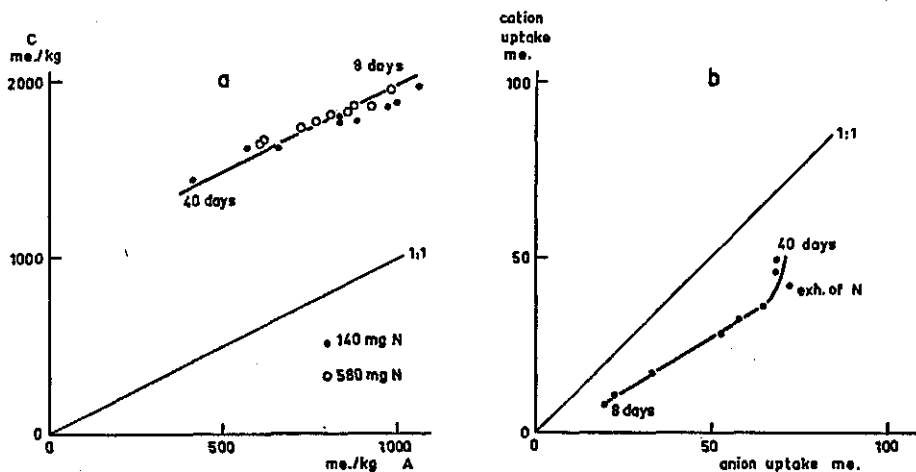


FIG. 17 a. The C and A content of the herbage of perennial rye-grass harvested between 8 and 40 days after application of 10 and 40 me. as  $\text{NH}_4\text{NO}_3$ .  
 b. The uptake of cations and anions in the herbage from 8 to 40 days after application of the nitrogen. From data of DIJKSHOORN (1958).

### 6.2.3 Periodic harvests

DIJKSHOORN (1958b) harvested perennial rye-grass on soil with 140 and 560 mg N as  $\text{NH}_4\text{NO}_3$  at four-day intervals from 8 to 40 days after the beginning of regrowth. Since the conditions were favorable for nitrification, this was comparable to a nitrate fertilization. The anion uptake is plotted against the cation uptake for the 140 mg N treatment in figure 17b.

With the first five harvests the anion uptake is considerably higher than the cation uptake. The ratio between cation uptake and anion uptake of 0.5 is maintained as long as the nitrate is not exhausted. After the fifth harvest the nitrate is exhausted and the cation uptake proceeds without concurrent anion uptake. These data illustrate that there is no direct coupling between cation and anion uptake.

The *C* and *A* contents for both treatments are plotted in figure 17a. The *A* content decreases with time because of nitrate exhaustion and because of dilution by growth of anions such as  $\text{Cl}^-$  (DIJKSHOORN, 1958a). Even with this large change in *A* content the (*C*—*A*) changed only from 925 to 1050 me./kg. Although the ratio between cation and anion uptake varied considerably during growth, the plants maintained a constant (*C*—*A*) content during the period of 40 days. The water content of the fresh herbage was 600 per cent at the 8th day and 375 per cent of the dry material at the 40th day. Hence, the (*C*—*A*) content varies considerably when expressed on a fresh weight or water basis.

### 6.2.4 Periodic harvests at two temperatures

DIJKSHOORN and 't HART (1957) studied the effect of temperature on the composition of perennial rye-grass. One set of plants grew at 20 °C for 11 days and at 10 °C thereafter; the other set grew at 10 °C for 11 days and at 20 °C thereafter. Samples were

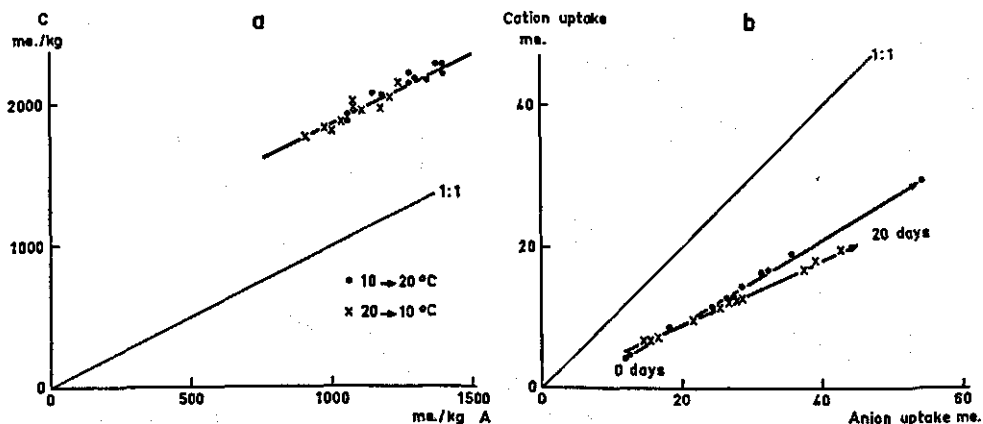


FIG. 18 a. The *C* and *A* content of the herbage of perennial rye-grass, harvested between 0 and 20 days after transfer from 10 to 20 and from 20 to 10 centigrades.

b. The uptake of cations and anions in the herbage from 0 to 20 days after the transfer.

From data of DIJKSHOORN and 't HART (1957), and not published data on nitrate.

taken from 2 to 20 days after the transfer. The final yields were 13 g/pot for the 10° → 20° plants and 11 g/pot for the 20° → 10° plants.

The anion uptake is plotted against the cation uptake in figure 18b. The ratio is 0.4 for the 20° → 10° plants and 0.6 for the 10° → 20° plants. The *C* and *A* contents are plotted against each other in figure 18a. The *A* content of the 10° → 20° plants increases and that of the 20° → 10° plants decreases during the periods of sampling, which indicates the different effect of temperature on growth and uptake. However, in both cases the (*C—A*) content remains closely at 900 me./kg, which again indicates regulation of the (*C—A*) content. The water content varied according to treatment and date of harvesting between 750 and 550 per cent of the dry material.

### 6.3 DISCUSSION

The (*C—A*) content of grass in the greenhouse experiments was found to be constant at the values of table 11.

TABLE 11 (*C—A*) contents in four experiments.

figure	15	16	17	18
grass	orchard	orchard	per. rye-	per. rye-
root med.	water	per. soil	soil	soil
year of exp.	1960	1958	1956	1956
temp. (°C)	20-25	20-25	20-25	20 10
( <i>C—A</i> ) me./kg	1100	1000 1000	950	900 900

The values are strikingly close together in spite of large treatment differences and in the same range as the (*C—A*) content of blue grass and wheat in the experiment of PIERCE and APPLEMAN (fig. 4). In short time experiments similar salt treatments as given here affect the (*C—A*) content of plant material considerably (section 2). Hence, the results can only be understood by supposing that these two grass species regulate the (*C—A*) content at a normal value roughly in the range between 1100 and 900 me./kg during their growth.

Since the (*C—A*) content equals the organic anion content, (fig. 4a) such plants have a neutral reaction ( $\text{pH} \approx 6$ ). Accordingly, the organic anions can accumulate in the shoot in the following ways. Organic anions formed in the roots are translocated upwards as their salts, or the nitrate ion is translocated as its salt, and metabolized in the shoot into organic N and organic anion.

An upward translocation of bicarbonates ( $\text{HCO}_3^- + \text{metallic cations}$ ) or a downward translocation of acids (inorganic or organic anions +  $\text{H}^+$ ) cannot contribute substantially to the organic anions in the shoot, since buffering substances (mainly phosphates) capable of buffering at pH 6 are commonly present at about 100 me./kg only, while (*C—A*) is about 1000 me./kg or more.



Therefore, a regulation of the organic anion or (C—A) content is possible only if sufficient organic anions and nitrate move upwards as their salts, and organic anions in excess of about 1000 me./kg (in the case of grass) move downward as their salts. Subsequently, decarboxylation takes place in the roots and the  $\text{HCO}_3^-$  produced exchanges with an anion from a neutral salt in the medium. Obviously, this kind of regulation fails when either the uptake of cations is too small or the uptake of inorganic anions which stay as such in the plant is too large. It may fail as well when metabolic reduction of nitrate proceeds at a low rate in the shoot. These conditions did not exist in the experiments of the present section, as is evident from the normal values for the (C—A) content of the plants. Their study requires other experiments with more extreme treatments, including those resulting in reduced plant growth as a result of stress on the ion balance.

## 7. IONIC BALANCE AND GROWTH OF BARLEY

### 7.1 SUMMARY

The relation between nutrient supply, composition and yield in barley is discussed. It is shown that, apart from any specific shortage of single ions, a stress on the (C—A) content leads to a reduction of the yield.

The effects of a replacement of K by Ca, of Cl excess and of Na and N fertilization are considered particularly.

### 7.2 DESIGN OF THE EXPERIMENT AND YIELDS

Ten to twelve barley plants were grown in pots containing 8.5 lbs of Evesboro sandy loam and harvested at the time of ear emergence. An initial nitrate supply of 30 me./pot appeared to be adequate.

With Ca, Mg and possibly Na-nitrate, K was in short supply. K can be supplied by (1) replacing the Ca, Mg or Na cation in the nitrate by K, (2) adding  $K_2SO_4$  and (3) adding KCl. Since the exchange capacity of the soil is about 250 me./pot and the pH about 6, a treatment with  $KHCO_3$  results in a soil with a reasonable K content without an increased anion content and gives no more information than, for instance, the experiment of figure 17.

To restrict the number of treatments without losing the possibility of comparing results in terms of replacement series, the K salts were added in amounts equivalent to the nitrate.

Hence the treatments were:

1.  $x$  me. $KNO_3$  +  $(30-x)$  me. $Ca(NO_3)_2$  with  $x = 0, 7.5, 15, 22.5$  and  $30$
2.  $x$  me. $KNO_3$  +  $(30-x)$  me. $NaNO_3$  with  $x = 0, 15$  and  $30$
3.  $x$  me. $KNO_3$  +  $(30-x)$  me. $Mg(NO_3)_2$  with  $x = 0, 15$  and  $30$
4.  $x$  me. $NaNO_3$  +  $(30-x)$  me. $Ca(NO_3)_2$  with  $x = 0, 15$  and  $30$
5.  $x$  me. $NaNO_3$  +  $(30-x)$  me. $Mg(NO_3)_2$  with  $x = 0, 15$  and  $30$
6.  $x$  me. $Ca(NO_3)_2$  +  $(30-x)$  me. $Mg(NO_3)_2$  with  $x = 0, 15$  and  $30$

To test the effects of additional salts, KCl,  $K_2SO_4$  and  $CaCl_2$  were added in amounts of 30 me./pot to the K-Ca replacement series. The nitrates of the four cations were also used in amounts of 10 and 20 me./pot to study the effect of nitrate application.

For salt damage the treatment 30 me. $NO_3$  + 30 me.Cl is most critical. It will be shown later that one of the main difficulties involved in heavy fertilization of poor soils is related to this combination. The soil received a liberal amount of Ca and Mg

phosphate. The experiment was made in triplicate and harvested at the time of ear emergence.

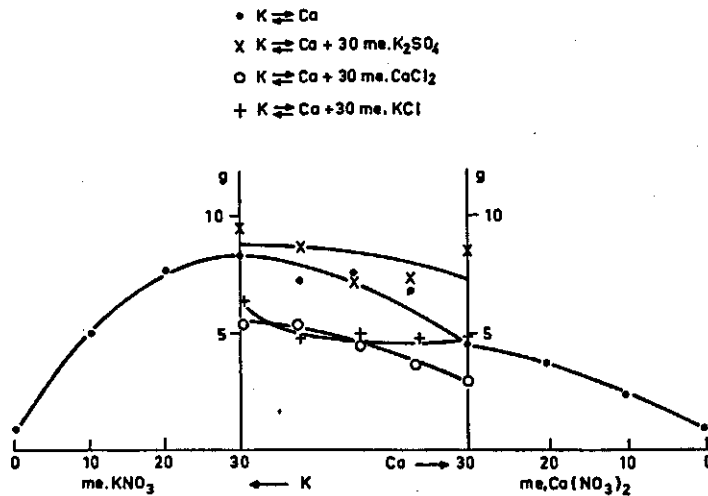


FIG. 19 Pot experiment with barley. The yield diagram.

The yields of the K-Ca treatments are summarized in figure 19. On the left the effect of the  $\text{KNO}_3$  and on the right the effect of the  $\text{Ca}(\text{NO}_3)_2$  application is presented. The middle part gives the effect of the K-Ca replacement with and without additional salts.

A nitrate supply of 30 me./pot is apparently sufficient. The treatment with Ca-nitrate yielded about half as much as the treatment with K-nitrate, which indicates a severe K-shortage. The K-Ca replacement series shows that 15 me.  $\text{KNO}_3$  + 15 me.  $\text{Ca}(\text{NO}_3)_2$  supplies sufficient K. The K shortage was relieved by the application of 30 me.  $\text{K}_2\text{SO}_4$ . The yield of the  $\text{KNO}_3$  +  $\text{K}_2\text{SO}_4$  treatment is higher than that of the  $\text{KNO}_3$  treatment, but this was irreproducible (compare figure 29). The K shortage was not relieved by the application of  $\text{KCl}$ ; the treatment  $\text{KNO}_3$  +  $\text{KCl}$  even gave a much lower yield than  $\text{KNO}_3$  only.

### 7.3 IONIC INTERRELATIONS

#### 7.3.1 Potassium-Calcium-replacement

The cation contents of the K-Ca replacement series are given in figure 20a. The K and Ca lines are curved in opposite directions and with decreasing K the Mg content increases in spite of the constant Mg supply. The shape of the curves suggests that all the K is taken up in competition with Ca and Mg. However, it has been shown (5.4, figure 11) that only a minor fraction of the K is taken up through a system

where the four cations compete and the major fraction enters the plant through a system operative for the K and Na ions.

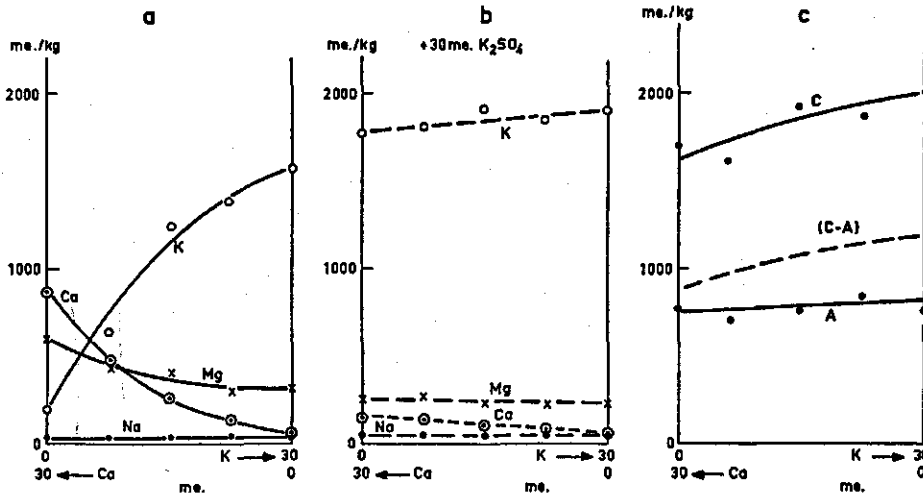


FIG. 20 Pot experiment with barley. K-Ca replacement series at an anion supply of 30 me.  $NO_3$   
a. in the absence of  $K_2SO_4$   
b. in the presence of  $K_2SO_4$   
c. the C, A and (C-A) content of the series in absence of  $K_2SO_4$ .

The difference between the experiments of figure 20 and figure 11 does not concern the competitive system, but the yield response. The yield was not affected in the experiment of figure 11, but in the present experiment the yield decreased with decreasing K content.

Suppose that with K the upward transport of (C-A) is 100 me. per day. This is sufficient to maintain a (C-A) content of 1000 me./kg at a growth rate of 100 grams per day. However, without K an upward transport of for instance, 50 me. (C-A) per day maintains a (C-A) content of 1000 me./kg at a growth rate of only 50 grams per day.

Hence, when a plant responds to a stress on the (C-A) content with a decrease in growth rate, this counteracts any sharp decrease in the (C-A) content and leads to an enhanced content of Ca and Mg. The yield reaction (figure 19) is therefore the reason that the (C-A) content decreases only from 1200 to 900 me./kg with the replacement of K by Ca (figure 20c).

By adding  $K_2SO_4$  the K content is higher over the whole range of the K-Ca replacement series (figure 20a and b). Since little  $SO_4$  is absorbed, the stress on the (C-A) content is relieved. The A content increased from 800 to 950 me./kg, but the C content increased from 1710 to 2230 me./kg, so that the (C-A) content was increased from 910 to 1280 me./kg by  $K_2SO_4$  in addition to Ca nitrate. The yield depression is of course absent after fertilization with  $K_2SO_4$ . The (C-A) content of

the  $\text{KNO}_3 + \text{K}_2\text{SO}_4$  treatments is  $2220 - 880 = 1340$  me./kg and only slightly higher than the (C—A) content of 1250 me./kg for the  $\text{KNO}_3$  treatment. This again illustrates plant regulation of the (C—A) content.

### 7.3.2 Application of chlorides

The above interpretation implies that, apart from specific functions, cations are necessary to keep the (C—A) content and thereby the organic anion content at their normal levels. RATHJE (1952) suggested this function of the cations, especially of the K ion. He arrived at this because yeast under the influence of sugar, and *Lemma* and *Chlorella* under the influence of light take up K ions and excrete Cl ions, this situation being reversed with exhaustion of sugar or with darkness. This change of the inorganic ion content has to go together with a change of the organic anion content, because neutrality is maintained. Since it is not possible to find specific functions for K at the rather high contents involved, RATHJE suggested that this cation is necessary in rather high concentrations because the organic anions are necessary for maintaining good growth.

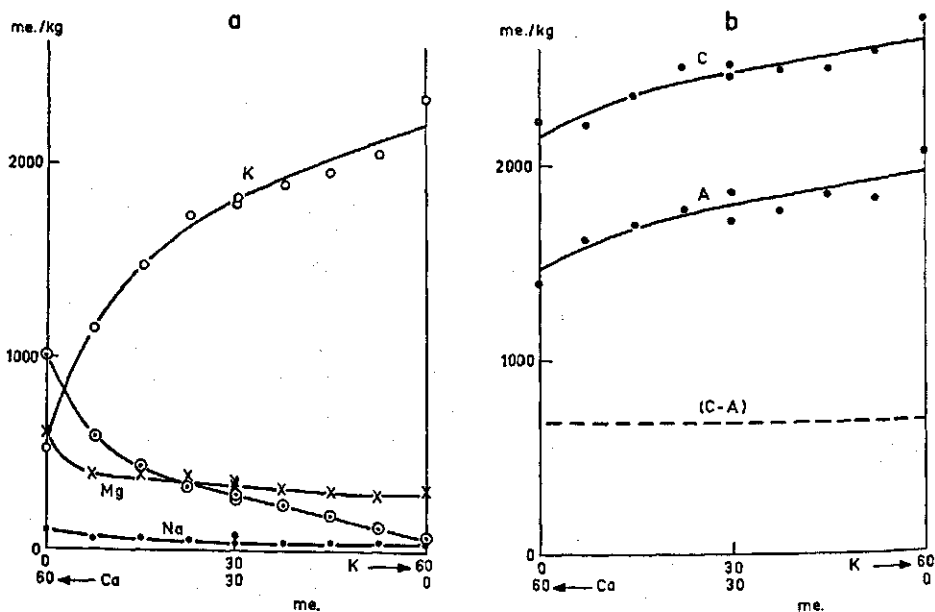


FIG. 21 Pot experiment with barley.

a. The K-Ca replacement diagram at 30 me. $\text{NO}_3$  plus 30 me.Cl.

b. The C, A and (C—A) content.

Any cation accompanied by an inorganic anion is useless in this respect, so that it is difficult to relieve a stress on the (C—A) content by the application of a fertilizer containing an anion that is readily absorbed and stays as such in the plant. This is illustrated by the results of the treatments with additional  $\text{KCl}$  and  $\text{CaCl}_2$ , summarized

as a K-Ca replacement series over a range of 60 me./pot in figures 21a and b. The anions were 30 me. $\text{NO}_3^-$  and 30 me. $\text{Cl}^-$ .

The Mg line is practically horizontal and the Ca line is straight except for the treatments 0 and 7.5 me.K. Since only these treatments have a lower yield than the other treatments with Cl (figure 19), this reaction of Mg and Ca is directly related to the yield response, as in figure 20.

With increasing K the C content increases (figure 21b). This is not associated with an increase of the (C—A) content but with an increase of the A content. Rather than relieving the stress on the (C—A) content, as with  $\text{K}_2\text{SO}_4$ , the KCl application increases the Cl content from 820 me./kg at 0 me.K to 1390 me./kg at 60 me.K. The (C—A) content is maintained at the low level of 660 me./kg, and this is accompanied by a considerable yield reduction. It should be noted that this does not imply that the stress on the (C—A) content is the only cause of yield reduction. Osmotic stresses in the soil due to  $\text{Cl}^-$  and  $\text{NO}_3^-$  application may have interfered as well (compare 8.7).

### 7.3.3 Fertilization with sodium

The element K has apparently two functions in the plant. It is essential as such and it functions as a positive charge accompanying organic anions, necessary for growth.

As an essential element K cannot be replaced by any other ion. According to LUNDEGÅRDH (1951) severe K deficiency develops at a level of about 200 me./kg. With a good supply of Na it is even possible to obtain small grain plants with a K content as low as 100 me./kg (BROESHART and VAN SCHOUWENBURG, 1961). These observations indicate that the minimum and essential level of K in small grains and grasses is between 100 and 200 me./kg.

The cations K, Na, Mg and Ca all function as positive charges. The Na ion is the most important for grasses and small grains grown at a low K level, because it can be taken up readily. For plant species such as plantain (5.3) the Ca and Mg ions may do as well in this respect. These two functions of K and the role of Na will be illustrated by means of the K-Na and the Ca(Mg)-Na replacement series of figure 22.

A comparison of the Na-nitrate and Ca(Mg)-nitrate treatments in figure 22b and c show that for both the (C—A) content is about 900 me./kg, the yield 3.5 g/pot, and the K content about 200 me./kg. This K content is about the minimum, so that the yield in both cases was mainly determined by the amount of K which was taken up. The ability of the plant to take up Na more readily than Ca(Mg) is reflected by the C content of 2300 me./kg for the Na treatment and 1650 me./kg for the Ca(Mg) treatment. But this high C content is accompanied not by a high (C—A) content, but by a high A content as with the Cl treatments (figure 21). The high A content is of course not a result of the high Cl, but of the high nitrate content which increased from 430 to 980 me./kg by replacing Ca(Mg) with Na. This inability to regulate at a high Na and a low K level will be studied in more detail in section 8.3.

The difference in the ionic balance of K deficient plants at high and low Na is reflected in their appearance. The plants with Ca(Mg) nitrate were stunted with a dry

matter content of 15 per cent, but developed normally otherwise. The plants with Na nitrate were long leaved and weak with a dry matter content of 12 per cent and had many more tillers. These two symptoms of K deficiency are described by WALLACE (1944). Apparently, the only effect of replacing Ca(Mg) nitrate with Na nitrate is that the plants change from one form of K deficiency to the other, and it can hardly be concluded from this part of the experiment that Na can replace K as a positive charge.

However, the treatment with 15 me. Ca(Mg) nitrate + 15 Na nitrate yielded 6.5 g/pot, and the plants had a (C—A) content of 1150 me./kg. Both were high compared with the 3.5 g/pot and the 900 me./kg for the Na-nitrate and the Ca(Mg) nitrate treatments. But the K-content was also at its minimum of 200 me./kg, so that K as an essential element was still limiting the yield. The remarkable difference is that on pots treated with the Na nitrate or with Ca(Mg) nitrate, the plants accumulated  $(200/1000) 3.5 = 0.7$  me.K, whereas they accumulated  $(200/1000) 6.5 = 1.3$  me.K on the pots treated with a mixture of both nitrate forms.

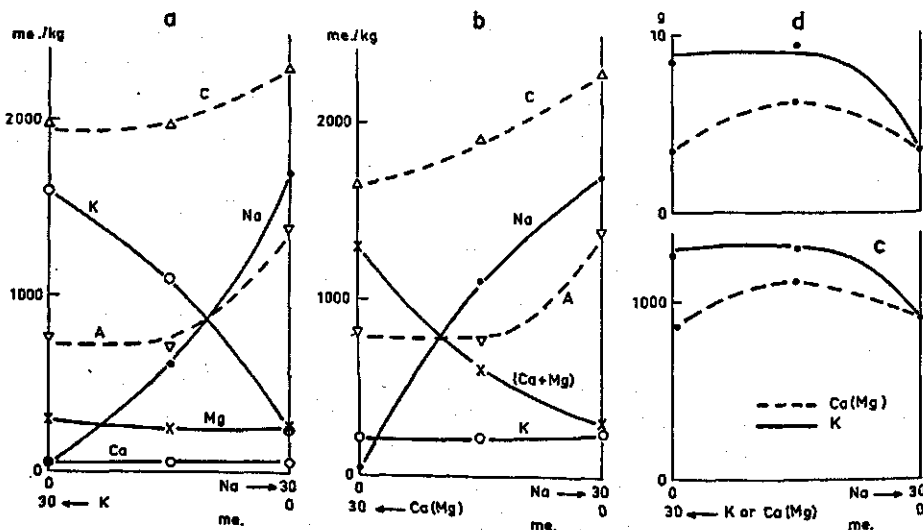


FIG. 22 Pot experiment with barley. The K-Na (a) and Ca(Mg)-Na (b) replacement series at 30 me.  $\text{NO}_3$ . The (C—A) contents and the yields are given in figure c and d. The Ca-Na and Mg-Na series gave about the same results, so that both are averaged to a Ca(Mg)-Na series.

Probably, the exploration of the soil in the pots treated with Ca(Mg) nitrate was hampered by the stunted growth and on the pots with Na-nitrate by the severe competition of Na with K (5.4). In the pots treated with the mixture of Ca(Mg) and Na nitrate the uptake of K was twice as large because the exploration for K was not hampered by stunted growth due to stress on the (C—A) content and not to such a large extent by competition of Na with K. This proves indeed that Na may replace K as a positive charge.

The cations K, Na, Mg and Ca are readily taken up by plantain (5.3). Preliminary experiments with this plant species showed that under conditions where grass yields are depressed because of K shortage, plantain grows normally.

#### 7.3.4 Fertilization with nitrogen

The ionic contents and the yields of the treatments 0, 10, 20 and 30 me. nitrate as its K or Ca salt are given in figure 23.

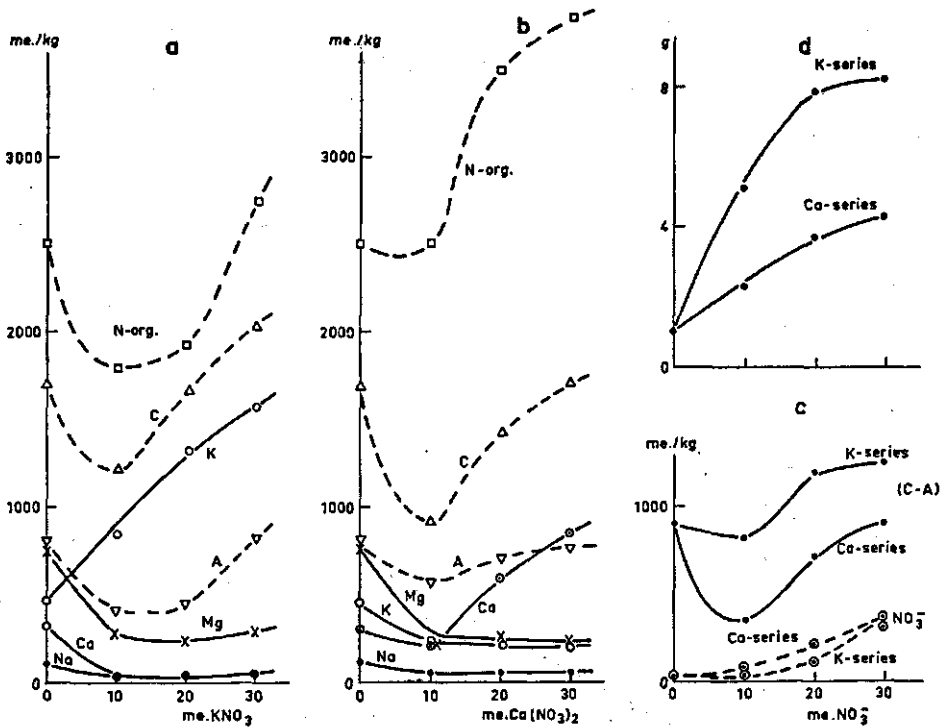


FIG. 23 Pot experiment with barley. The  $KNO_3$  (a) and  $Ca(NO_3)_2$  (b) concentration series. The (C—A) contents, the  $NO_3^-$  content and the yield are given in figure c and d.

The unfertilized plants were very stunted and the C and A contents were high because of the absence of any dilution by growth. The nitrate content was low and bad growth was in the first place due to nitrogen shortage. The (C—A) content was only 900 me./kg, probably because at this low supply any nitrate absorbed is metabolized in the roots. The growth was stunted from the beginning, which indicates that the stress on the (C—A) content existed from the beginning. For this reason, small cells are formed which have a high nitrogen content in spite of the nitrogen shortage.

With 10 me. $KNO_3$  the growth appeared to be the same as with 30 me. $KNO_3$  during the first part of the growth period, but later on the growth was retarded because of nitrogen shortage, as judged from the low  $NO_3^-$  content and an N and K uptake of



9 me. and 4 me., respectively, from a supply of 10 me. The (*C—A*) content was only 900 me./kg probably because of the absence of nitrate reduction in the leaves during the later part of the growing period. During the first part growth proceeded normally and a normal (*C—A*) content was probably maintained. At this stage plants with normal sized cells of a normal protein content were formed. The transition from higher to lower N content as the result of N application at low N levels has been frequently observed.

With 10 me.  $\text{Ca}(\text{NO}_3)_2$  the N-uptake was only 6.5 me. and the plants were stunted because of severe K shortage, as appears from the low K content and the very low (*C—A*) content. With increasing  $\text{Ca}(\text{NO}_3)_2$  the yield increased because some more K became available. This may be due to exchange reactions between the soil and the soil solution.

#### 7.4 (*C—A*) CONTENT AND YIELD

The *C* and *A* contents of the plants of all treatments are given in figure 24. The normal value of the (*C—A*) content is apparently somewhat higher than in grasses (section 6.3) at around 1250 me./kg, although many treatments resulted in lower (*C—A*) contents.

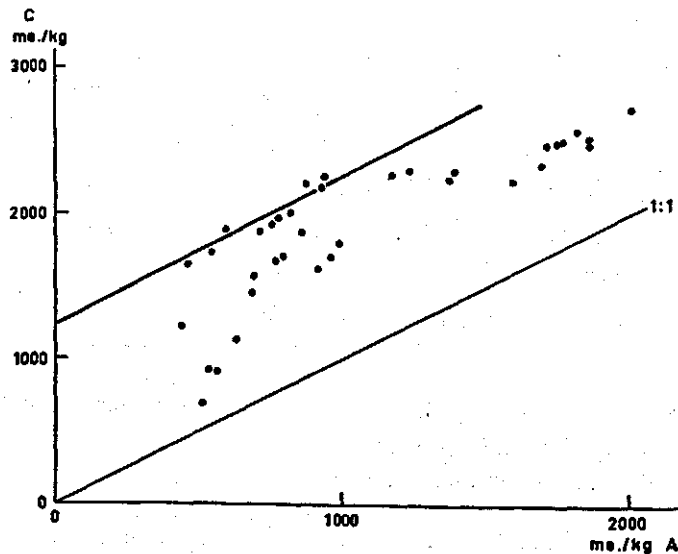


FIG. 24 Pot experiment with barley. The relation between the *C* and *A* contents for all treatments.

The (*C—A*) contents and the yields are related as shown in figure 25. It could be that low yields are associated with a low water content of the plants and, because the ions are mainly in the plant juice, also with a low (*C—A*) content. However, the water

content of plants with a yield of 9 grams per pot was 675 per cent and of plants with 3 grams yield was 525 per cent of the dry material, whereas (C—A) varied from 1200 to 600 me./kg within the same yield range.

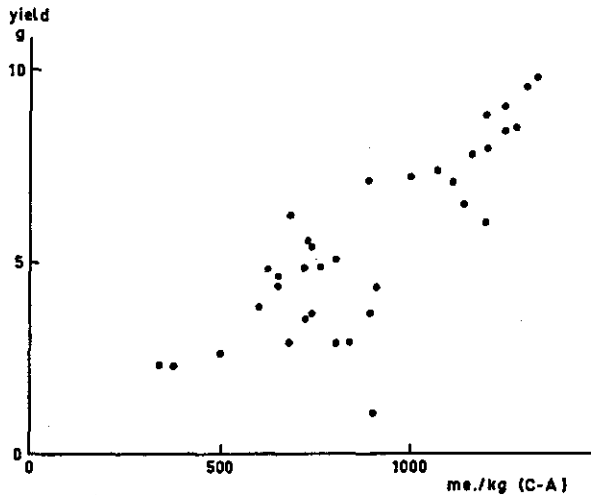


FIG. 25 Pot experiment with barley. The yield and the (C—A) content for all treatments.

Therefore, the relation between (C—A) and yield must be understood in another way. Either, the treatment affects the yield and the yield affects the (C—A) content, or the treatment results in a stress on the (C—A) content and this stress affects the yield. Experiments with more extreme treatments are required to distinguish between both views. If, in addition, it is only possible to combine a high yield and a low (C—A) content, a high yield is *one* of the conditions for a normal (C—A) content. However, if in addition it is only possible to combine a low yield with normal (C—A), a normal (C—A) content is *one* of the conditions for a high yield.

## 8 FURTHER EXPERTIMENTS OF THE RELATION BETWEEN NUTRIENT SUPPLY, (C-A) CONTENT AND YIELD

### 8.1 SUMMARY

A distinction is made between the effect of the nutrient status of the plant on the growth rate and the correlation between nutrient status and yield.

Subsequently it is shown that a normal (C-A) content is one of the conditions for maximal growth. Na fertilization, Cl application and the relation between  $\text{NH}_4$  fertilization, (C-A) content and yield is considered more in detail.

### 8.2 NUTRIENT STATUS, GROWTH AND YIELD

At the time of sampling, a functional relation may exist between the nutrient status and the growth rate of a plant. But the relation between the nutrient status and the yield at the time of sampling is, at most correlative, because the yield is the growth rate integrated over the whole growing period.

In figure 26, three growth curves are given on an arbitrary scale. It is supposed that the growing conditions are constant functions of time. Curve A represents the yield on a field with a plant species with a normal growth. During the early part of the growing period, new assimilatory products are used to form new leaves and these leaves contribute to light utilization. Hence, the growth curve is more or less exponential. At a certain stage, here at the weight 5 and time 3.3, all the light is intercepted, i.e. the crop surface is closed. Thenceforth the yield increases linearly with time, until respirational losses or senescence begins to interfere. The smaller the plant density, the later the onset of the straight line part of the curve. Single growing plants may show a similar straight line portion when a stage is reached without net increase of leaf area.

Curve B represents the growth of a crop of a plant species with a net assimilation rate at one-half of the net assimilation rate of the plants A and, at the onset of this difference (time 0), of the same size. Because plants B assimilate at a much slower rate, a difference in size develops rather quickly so that at the time 5.7 instead of 3.3, the closed crop surface is established. After that the growth rate of crop B does not change with time and is only one-half of the growth rate of crop A. The yields of B and A will be near to this proportion as long as senescence, etc. do not disturb growth. Hence, in this case, the ultimate ratio of the yields corresponds quite well to the ratio of the growth rates.

In the case of plant species C and A, the growth rate of C is again one-half of that of A, but now because for each gram of dry matter produced only half of the leaf surface is formed. At the beginning the weight increase of plants A and C is about the same because the leaves present at time 0 assimilate at the same rate. However, plants C stay behind in due course because less leaf area is formed. The weight of 5 units is reached at time 4.3. At this time crop A, having a yield of about 10, already has a closed crop surface. Crop C is still open because of the retarded leaf formation,

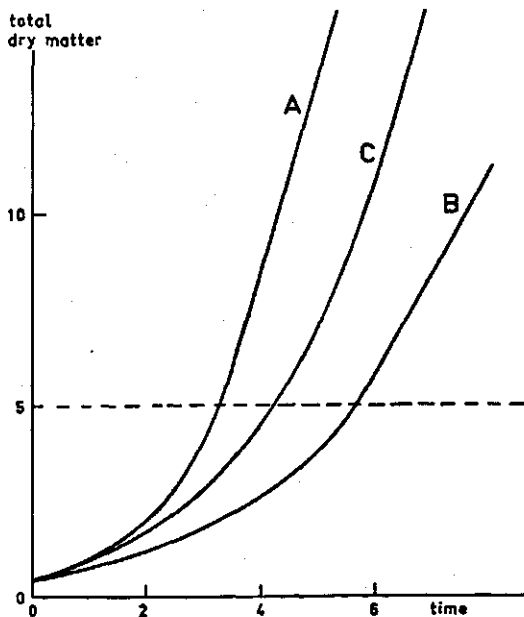


FIG. 26 Three growth curves.

and this crop proceeds therefore to grow in a more or less exponential fashion and catches up with crop A. Around time 6, also crop C intercepts all the light and from then on both crops grow at the same linear rate, because the net assimilation rate is the same. The difference in dry matter production of about 6 units remains unchanged but the relative difference decreases very rapidly with time. Hence, only at around time 4 is the yield ratio about equal to the ratio of the growth rates, whilst before and thereafter the yield ratio is much lower. In this case the yield differences reflect the growth differences only, if the onset of the growth difference occurs in an early stage and if the crop is harvested at the end of the period of exponential growth.

WATSON (1952) studied the effect of nutrients on growth by growth analysis. He found that an effect of nutrients manifests itself first in the leaf development and that the net assimilation rate is only affected in cases of more extreme growth reduction. This conclusion was confirmed by DE WIT (1958) in a study on the effect of the

nutrient status of plants on the transpiration ratio. Therefore, the effect of nutrients on the growth of a crop is better pictured by the growth curves C and A, than by the curves B and A of figure 26.

Fertilizer experiments with the purpose of relating nutrient status and growth rates on the basis of yields must therefore be carried out with plants growing exponentially. On the other hand, densely planted grass with a high leaf density on a reasonably fertile soil and grown for some weeks very likely shows small yield effects of treatments (10.2).

### 8.3 SHORTAGE OF MICROELEMENTS

The low (C—A) contents of figure 25 may result from bad growth, or bad growth from a stress on the (C—A) content (7.4). Apparently, varying the supply of macronutrients is not a suitable method for distinguishing between both possibilities. But, growth may also be varied by varying the micronutrients at constant supply of the macronutrients.

SCHARRER and JUNG (1956) grew corn on a nutrient solution in which the microelements Mn, Cu, Zn, Fe, B, Mo and Co were present in varying quantities. Low yields were obtained by adding Co in excess and by omitting one of the other microelements. The effect of the growth rate on the (C—A) content can be studied in this way.

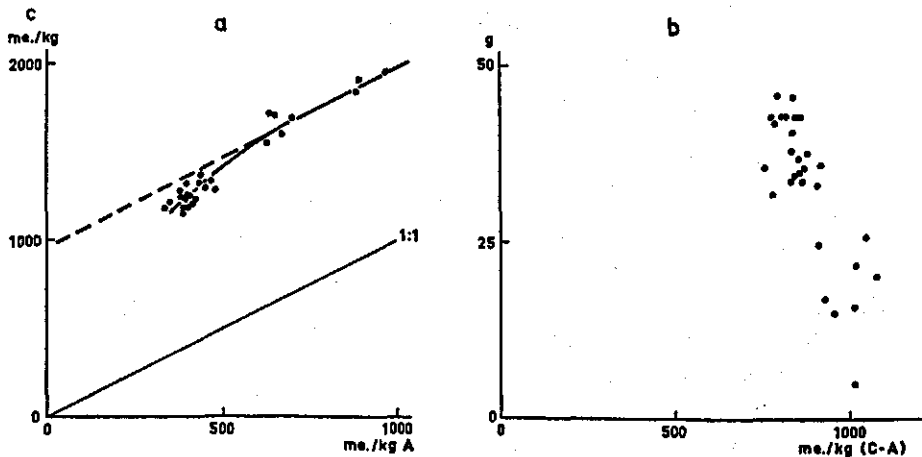


FIG. 27 a. The C and A contents of maize, supplied with different amounts of micro-nutrients. b. The yields and (C—A) contents. From data of SCHARRER and JUNG (1956).

The C and A contents are given in figure 27a. The growth differences resulted in different degrees of exhaustion, which in turn caused different C and A contents. The

corn plants maintained, however, their (C—A) content close to 1000 me./kg. The cluster of observations around 400 me./kg of A concerns plants with good growth. The (C—A) content is somewhat lower here than with the other plants, probably because nitrogen, as judged by the zero NO<sub>3</sub> content, was in rather short supply. The yield and the (C—A) content are plotted in figure 27b. The (C—A) content is close to 1000 me./kg whereas the yield varied markedly. Hence, the (C—A) content is not a function of growth. Combined with the data of figure 24, a normal (C—A) content appears to be one of the conditions necessary for maintenance of a good growth rate.

This conclusion was confirmed by a similar experiment of SCHARRER and JUNG (1956) with horse beans, although Fe-shortage resulted there in an excessively high (C—A) content. It is known that iron induced chlorosis may go together with a high organic anion content.

#### 8.4 POTASSIUM-SODIUM REPLACEMENT

The normal (C—A) content of barley is maintained over a wider range when K is replaced by Na (figure 22a and c), than when K is replaced by Ca (figure 20a and c). However, with extreme K shortage in the presence of Na, weak barley plants developed which had lost their ability to maintain the normal (C—A) content.

The change of contents with K shortage and Na excess is shown more in detail by results of VAN DEN BERGH (IBS, Wageningen). Two grass species, perennial rye-grass and foxtail, grown together.

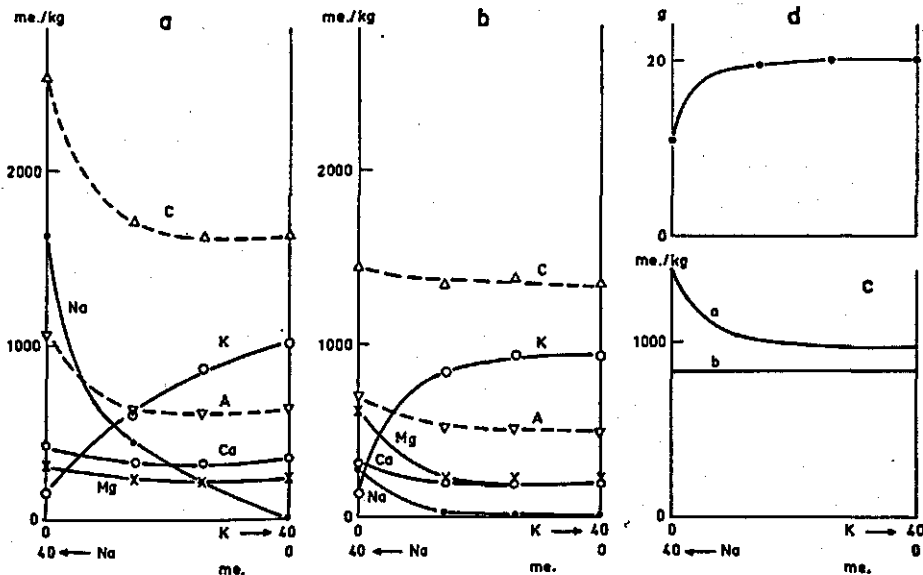


FIG. 28 K-Na replacement diagrams of perennial rye-grass (a) and foxtail (b) grown together. The (C—A) contents and the yields are given in figure c and d. Data of VAN DEN BERGH, IBS, Wageningen.

and foxtail (*Alopecurus pratensis*), were grown in mixed culture in containers and K exhaustion was achieved by cutting a few times before applying the treatments. Mixed culture ensures that the nutrient supply is the same for both species throughout the growing period.

The results are given in figure 28. The (C—A) content of perennial rye-grass remains constant at 1000 me./kg over a wide range. With 40 me.  $\text{NaNO}_3$  the K content is only 140 me./kg so that the yield is completely governed by the K uptake. Under these conditions perennial rye-grass accumulates excessive amounts of Na and anions. This was also the case in the experiment of figure 22, but there it was associated with a (C—A) content lower than normal, whereas it is above normal in figure 28 for perennial rye-grass.

Referring to the regulatory mechanism postulated in 6.3, it seems that the plants are unable to transport cations other than K readily downwards. The breakdown of regulation at high Na and low K does not occur in the foxtail of figure 28, probably because this species cannot take up Na at a rate comparable to that of K.

### 8.5 APPLICATION OF CHLORIDES

The yield of barley fertilized with 30 me.  $\text{Ca}(\text{NO}_3)_2$  was unchanged by the addition of 30 me. KCl. This was associated with the difficulty of relieving the stress on the (C—A) content by giving K together with Cl. However, the salt levels in the soil were so high that osmotic damage might have interfered.

To study the problem in more detail oats were grown under similar conditions as the barley plants of the experiment of section 7. The pots were fertilized with 20 me.

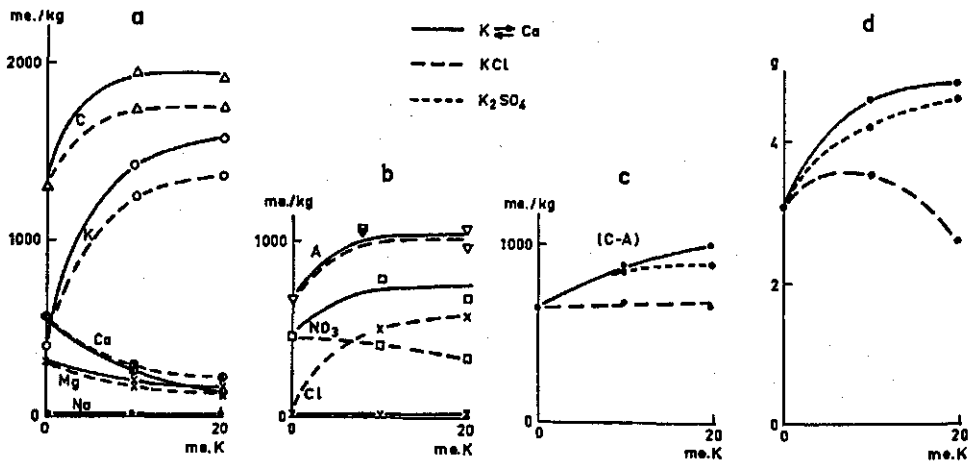


FIG. 29 Pot experiment with oats. The cation contents (a) and anion contents (b) at three levels of a K for Ca and a KCl application. The (C—A) contents and the yields for these treatments and for application of  $\text{K}_2\text{SO}_4$  are given in the figures c and d.

NO<sub>3</sub>. The K was applied by replacing the Ca of Ca nitrate with K, or by applying KCl or K<sub>2</sub>SO<sub>4</sub> up to amounts of 20 me. These are levels at which, according to the experience with barley, no serious osmotic damage occurs.

The (C—A) contents (figure 29c) and the yields (figure 29d) of the plants supplied with K instead of Ca and in the form of sulphate are practically the same. The sulphate treatments yielded somewhat less, but this difference between both forms of K application appeared unreproducible (compare figure 19).

The results of the K for Ca and KCl treatments deserve a detailed comparison. The (C—A) content of the plants fertilized with Ca(NO<sub>3</sub>)<sub>2</sub> is only 650 me./kg. Since the K content is 400 me./kg, these plants suffered from a stress on the (C—A) content rather than from a specific K shortage. The stress is relieved by the KforCa treatment but not by the KCl treatment (figure 29c). Likewise, the yield of the KCl treatment is lower over the whole range (figure 29d).

The stress of the (C—A) content in case of Cl application was associated with an increased A content in the barley experiment. However, in this experiment it is associated with a lower C content, and the same A content compared with the K for Ca treatment. A further comparison of the results shows that with 20 me.K as K nitrate the nitrate content is high and the Cl content low and that with 20 me. K as KCl Cl is high and NO<sub>3</sub> correspondingly lower (figure 29b). The organic N content is 2500 and 2100 me./kg for the KNO<sub>3</sub> and KCl treatments, respectively. The presence of Cl resulted in a lower transport of nitrates and organic anions to the top, so that the (C—A) content was not maintained at its normal value of 950 me./kg (section 6.3).

As discussed in 7.3.2, K has two functions in the plant: a specific function and its function as a positive charge accompanying the organic anions. KNO<sub>3</sub>, K<sub>2</sub>SO<sub>4</sub> and K-clay are good sources to meet the requirements for both functions. When K is

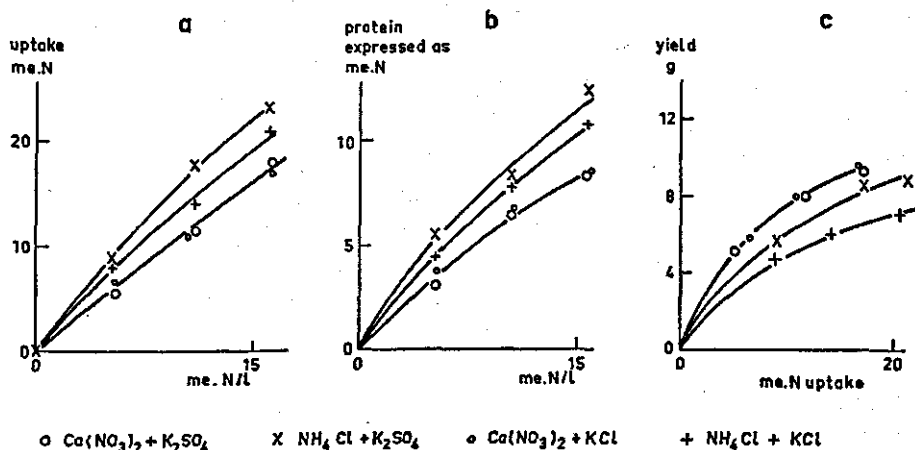


FIG. 30 The effect of N-application on the N-uptake (a) and the protein production (b) and the relation between N uptake and yield (c) of rape seed, fertilized with nitrogen as Ca(NO<sub>3</sub>)<sub>2</sub> or NH<sub>4</sub>Cl with K<sub>2</sub>SO<sub>4</sub> or KCl. From data of BUCHNER (1952).



below the specific requirement of 200 me./kg KCl is also an adequate K source. When K is mainly required as a positive charge, accompanying the anions, KCl may suffice as long as K is absorbed in a sufficient excess to Cl, which again depends on the supply with  $\text{NO}_3$  and other ions.

In the soil, Cl is easily transported with the water. During this transport the accompanying cations are subject to exchange with other cations, mainly Ca. Hence, Cl, applied as KCl, reaches the roots mainly as  $\text{CaCl}_2$ , so that a KCl application to the soil may be more harmful than KCl supplied in solution. If there is leaching the same process leads to a removal of Cl with Ca, whereas K is retained.

## 8.6 AMMONIUM FERTILIZATION

Nitrate is readily absorbed and transformed to the reduction stage of ammonia before it is assimilated into organic compounds, and ammonium is also readily absorbed. Any differences in response to either form of nitrogen are therefore related to their different effects on the ionic balance of plant and solution (STREET and SHEAT, 1958; NIGHTINGALE, 1937).

Some effects of ammonium fertilization are illustrated in figure 30, based on data of BUCHNER (1952), who supplied rape plants with different amounts of  $\text{NH}_4\text{Cl}$  and  $\text{Ca}(\text{NO}_3)_2$  in nutrient solutions, adding K in the form of KCl or  $\text{K}_2\text{SO}_4$ . The relation between applied amount of nitrogen and uptake of N is given in figure 30a. The uptake of N is highest with  $(\text{NH}_4\text{Cl} + \text{K}_2\text{SO}_4)$  and the lowest with  $\text{Ca}(\text{NO}_3)_2$ . Likewise the protein production (figure 30b) is the highest with  $(\text{NH}_4\text{Cl} + \text{K}_2\text{SO}_4)$ . Ammonium is apparently the better source of N for protein production.

But it is seen in figure 30c that the relation between dry matter production and N uptake is by far the most favorable for the treatments with nitrate. The plants with nitrate produced about 8 g of dry matter and those with  $(\text{NH}_4\text{Cl} + \text{KCl})$  only 5 g of dry matter at an uptake of 10 me.N. Even though ammonia is a good nitrogen source, the plants treated with this ion did not grow very well, especially when the K was given as KCl.

Other data, mentioned in 8.3, suggest that plants can maintain their (C—A) content in the tops only if a part of the nitrogen is transported upward as  $\text{NO}_3^-$ . Consequently, with ammonia as the sole nitrogen source a stress on the (C—A) content may develop. Moreover, the ammonium ion may compete with the K ion during uptake. Since the N from the ammonium ion is incorporated in the protein and its positive charge released as  $\text{H}^+$ , the ammonium ion is of no use as far as the maintenance of the (C—A) content is concerned.

The competitive effect of  $\text{NH}_4$  on the uptake of Rb is shown by an experiment with excised roots of barley given in figure 31. TROMP (1962) studied the interactions in the absorption of ammonium, potassium and sodium by roots of wheat plants. He showed that the K uptake is reduced to one-half or less by the concurrent uptake of

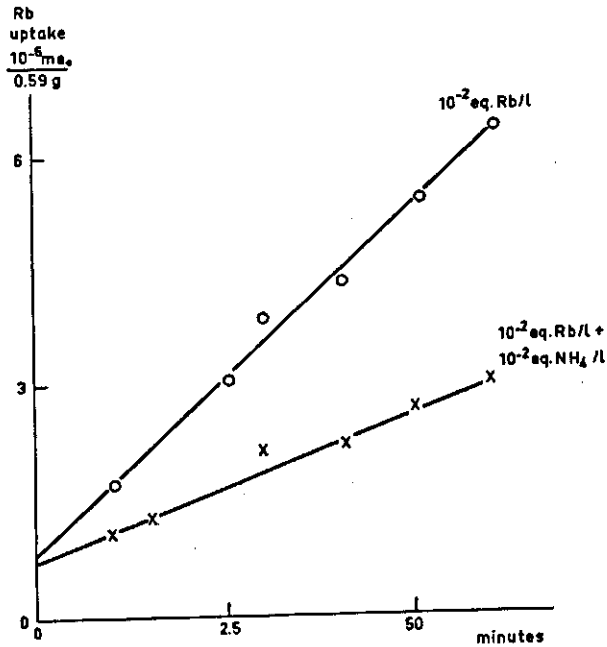


FIG. 31 The effect of the presence of  $\text{NH}_4\text{Cl}$  on the Rb uptake by excised barley roots from  $\text{RbCl}$

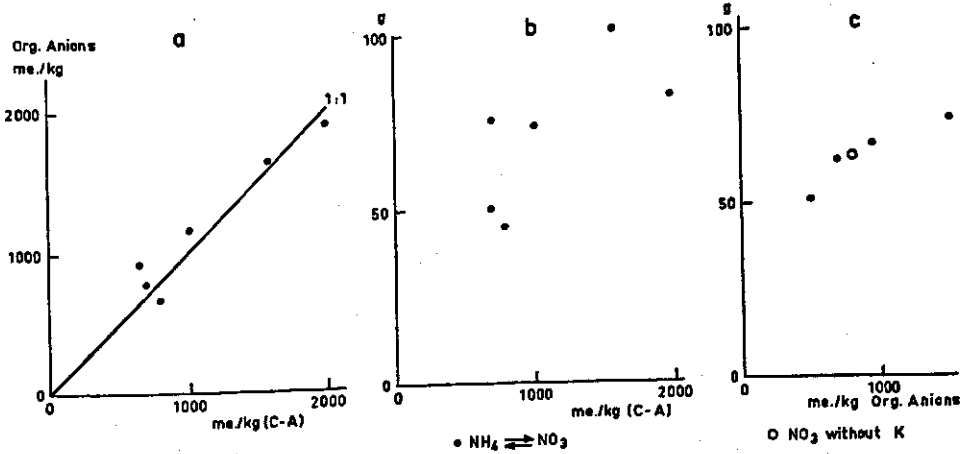


FIG. 32 The organic anion contents and the (C—A) contents (a) and the (C—A) contents and yields (b) for tobacco fertilized with ammonium and nitrate in different proportions. Data of VICKERY *et al.* (1940).  
c. The yields and organic anion contents of *Bryophyllum* fertilized with ammonium and nitrate in different proportions and with nitrate in the absence of potassium. Data of PUCHER *et al.* (1947).

ammonium. These observations suggest that ammonium as a nitrogen source may lead to plants with a stress on the (C—A) content and therefore to plants with a lower yield.

Some direct information on this subject can be obtained from data of VICKERY *et al.* (1940) and PUCHER *et al.* (1947), who cultivated tobacco and *Bryophyllum calycinum* with varying amounts of ammonium and nitrate in the nutrient medium. The (C—A) content and the organic anion content of the leaves of tobacco are given in figure 32a. The observations are around the 1 : 1 line over the whole range from 100% ammonia to 100% nitrate so that this relation found for nitrate appears to be essentially the same for ammonium. The relation between the yield and the (C—A) content of tobacco is given in figure 32b. With high ammonium, the yield is 50 g and the (C—A) content about 800 me./kg. High yields are obtained only at (C—A) contents around 1800 me./kg, reached by giving nitrogen mainly in the form of nitrate. A similar relation was found between the yield and organic anion content of *Bryophyllum* (figure 32c), which was obtained by varying the form of nitrogen supply or by omitting potassium from the solution with nitrate.

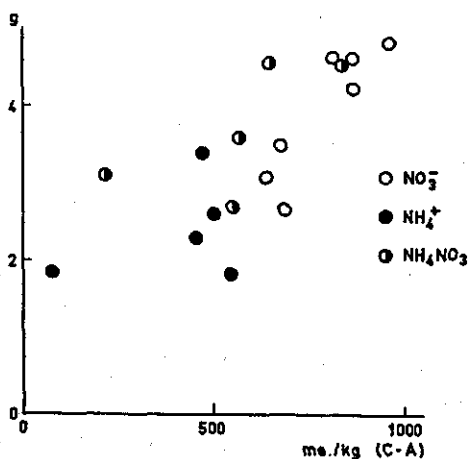


FIG. 33 Pot experiment with oats. Yields and (C—A) contents of oats fertilized with N as NH<sub>4</sub>, NH<sub>4</sub>NO<sub>3</sub> and NO<sub>3</sub>.

The experiment with oats discussed in 8.3 included also treatments with nitrogen as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and NH<sub>4</sub>NO<sub>3</sub> at the rate of 20 me. and K at the rates of 0, 10 and 20 me. per pot as the chlorides or sulphates. Yields and (C—A) contents of all treatments are summarized in figure 33. Whatever the fertilizer treatment, good growth can be expected only if the (C—A) content is maintained around its normal value. The yield of 4.5 g at a (C—A) content of 650 me./kg for the treatment 20 me.N as NH<sub>4</sub>NO<sub>3</sub> + 10 me.K<sub>2</sub>SO<sub>4</sub> and the data of figures 32b and 32c indicate that the (C—A) content may be less critical when ammonium and nitrate are applied together.

SCHARRER and JUNG (1955) reported some data on the composition of perennial rye-grass, harvested far in the flowering stage. The *C* and *A* contents are given in figure 34. The normal (*C—A*) content at this advanced stage is apparently about

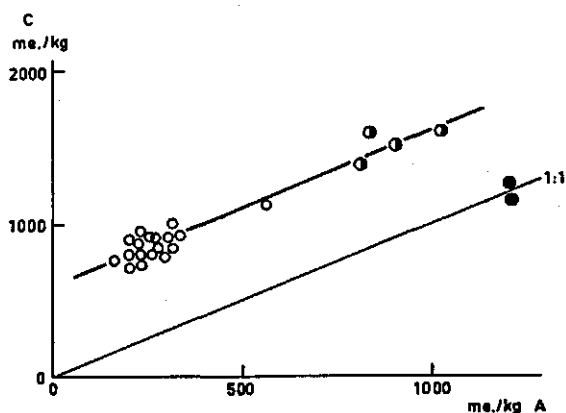


FIG. 34 The relation between the *C* and *A* content of perennial rye grass far in the flowering stage, fertilized with N as  $\text{NO}_3$ ,  $\text{NH}_4\text{NO}_3$  and  $\text{NH}_4$  fertilizer. From data of SCHARRER and JUNG (1955).

500 me./kg. It was reported that the plants fertilized with  $\text{NH}_4\text{NO}_3$  in combination with other fertilizers had a lower yield than the plants with nitrate only and that the plants with ammonium had very low yields. The  $\text{NH}_4\text{NO}_3$  plants maintained the normal (*C—A*) content at a low yield, which shows again that a normal (*C—A*) content is only one of the conditions for a good yield. However, the plants fertilized with  $\text{NH}_4$ -salts had both a low yield and a low (*C—A*) content.

## 8.7 BUCKWHEAT

The plant species discussed up to now have a normal (*C—A*) content of about 1000 me./kg in the vegetative stage. The data of PIERCE and APPLEMAN (figure 4) show that there are plant species such as spinach, buckwheat and beets, with an organic anion content of about 5000 me./kg.

In an experiment with buckwheat it was studied to what extent this high (*C—A*) content is a condition for good growth.

The results of the K-Ca replacement series with the nitrate at 20 me. is given in figure 35. The cation content (figure 35a) increases from the already high level of 2000 to 4400 me./kg with increasing K. The anion content (figure 35b) remains constant around 340 me./kg and the (*C—A*) content increases from about 1700 to 4000 me./kg (figure 35c). The yield increases from 2.2 to 5.3 grams (figure 35d), which indicates that this high (*C—A*) content of 4000 me./kg and hence a K content around this value are necessary for good growth.

The plants fertilized with 20 me.  $\text{Ca}(\text{NO}_3)_2$  plus 20 me.  $\text{K}_2\text{SO}_4$  yielded 4.5 g and had a (C—A) content of about 5000 me./kg, whereas the ammonium nitrate treatments yielded 2 grams with a (C—A) content of about 1200 me./kg. Likewise 20 me.  $\text{Ca}(\text{NO}_3)_2$  plus 20 me.  $\text{CaCl}_2$  yielded 1.3 g with a (C—A) content of only 2200 me./kg. In this respect buckwheat responds about the same as the oats (8.5).

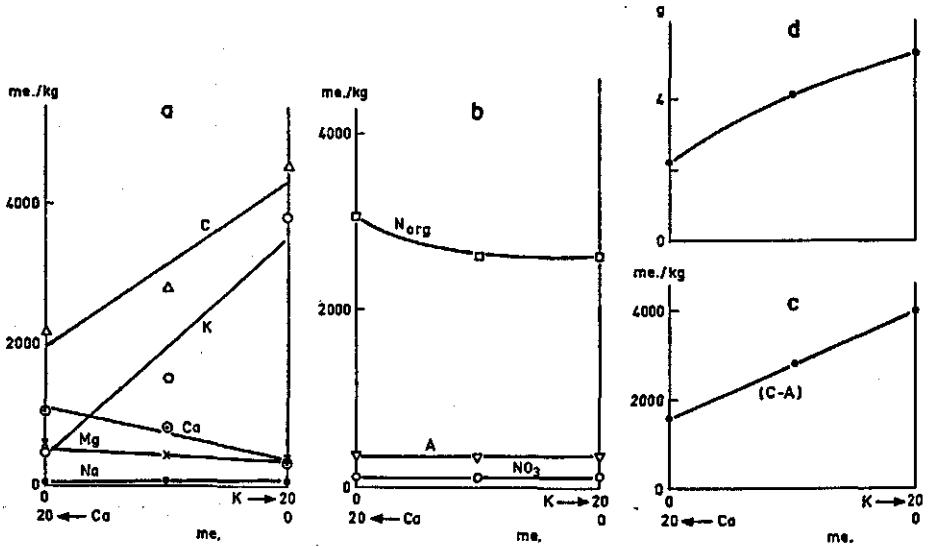


FIG. 35 The cation content (a), anion content (b), the (C—A) content (c) and the yield (d) of buckwheat grown on a K—Ca replacement series.

The plants treated with 20 me.  $\text{KCl}$  plus 20 me.  $\text{Ca}(\text{NO}_3)_2$  or 20 me.  $\text{KNO}_3$  had an *A* content of 800 me./kg, and a *C* content of 5350 me./kg. The (C—A) content was therefore about normal at 4500 me./kg, but the yield was only 3.2 grams. The yield was probably reduced by an osmotic stress in the soil, whereas the relative uptakes of the ions appeared to be such that the normal (C—A) content could be maintained. This result shows again that a normal (C—A) content is one, but not the only one condition for good growth.

# 9 IONIC BALANCE OF PLANT AND SOIL

## 9.1 SUMMARY

Well-nourished plants have either an external alkaline or an external acidic effect. An external acidic effect is associated with a net movement of metallic cations from the soil complex to the soil solution, whereas an external alkaline effect is associated with a net movement of metallic cations from the soil solution to the soil complex.

## 9.2 EXTERNAL ALKALINE AND ACIDIC EFFECTS

The cation and anion uptake by good growing grass is given in figure 17b. As long as nitrate is not exhausted the anions are taken up in excess to the cations. During this process of excess anion uptake, electroneutrality is maintained by a net uptake of  $H^+$  ions. This external alkaline effect with nutrient solutions is reflected in a decrease of the  $H^+$  concentration of the solution. In the presence of the soil complex this decrease in  $H^+$  concentration is buffered by the exchange of  $H^+$  from the soil complex with metallic cations from the soil solution. The process is depicted in the left-hand part of the diagram of figure 36. During excess anion uptake there is a movement of metallic cations to both the plant and the soil complex, and the soil complex is not a source, but a sink for metallic cations. WALKER (1960) points to the shift of metallic

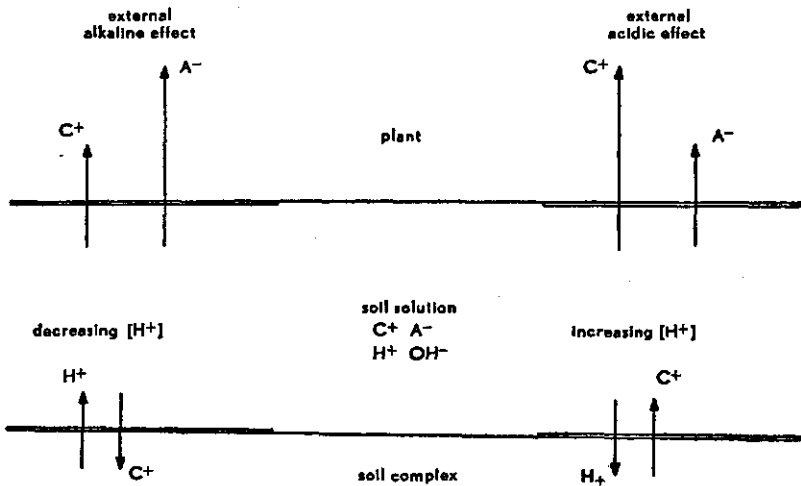


FIG. 36 Ionic balance of plant and soil.

cations from the soil solution to the soil complex as a result of the external alkaline effect. During further growth nitrate eventually comes to exhaustion and from there on cations are taken up in excess of anions. In figure 17b the curve does not intersect the 1 : 1 line so that the net external effect remains alkaline.

Irrespective of the nutritional status the organic N content of grass always exceeds the ( $C-A$ ) content so that grass always has an external alkaline effect. This also holds for the barley of figure 23 and the oats of figure 29, both of which had an organic N content of around 2500 me./kg and a ( $C-A$ ) content of at the most 1250 me./kg.

The buckwheat plants of figure 35 took up about 4000 me./kg cations and 3000 me./kg anions when fertilized with  $KNO_3$ . During the process of excess cation uptake electroneutrality is maintained by a net release of  $H^+$  ions. This external acidic effect is, in nutrient solutions, reflected in an increase of the  $H^+$  concentration of the solution. In the presence of the soil complex this increase in the  $H^+$  concentration is buffered by the exchange of metallic cations from the soil complex with  $H^+$  from the soil solution. This process is depicted in the right-hand part of the diagram of figure 36. During excess cation uptake there is a movement of metallic cations from the soil complex to the soil solution to the plant. In this case the soil complex is a source of metallic cations. When fertilized with  $Ca(NO_3)_2$  the buckwheat plants of figure 35 took up about 2000 me./kg cations and about 3500 me./kg anions and, therefore, had an external alkaline effect. Such an inversion of the external effect as a result of a change of the nutritional status can occur only when the normal ( $C-A$ ) content is of the same order of magnitude as the organic N content.

## 10 A TEST ON THE MACRONUTRITIONAL STATUS OF GRASS

### 10.1 SUMMARY

A block diagram for evaluating the nutritional status of grass plants is given. Its application is illustrated with some examples.

### 10.2 SPECIFIC REQUIREMENTS

As discussed in section 1, N and S are sufficient if the  $\text{NO}_3^-$  and  $\text{SO}_4^{--}$  contents of the plant are higher than 100 and 20 me./kg. Adequacy of P supply is indicated by a total  $\text{H}_2\text{PO}_4^-$  content higher than 70 me./kg. As a macroelement  $\text{Cl}^-$  is not essential.

In the case of  $\text{NH}_4$  supply an organic N content higher than 2500 me./kg indicates adequate N supply, irrespective of the  $\text{NO}_3^-$  content (VAN BURG, 1962).

Contents of *A* higher than 250 me./kg are common and do not affect growth provided that the ionic balance is maintained. Contents of *A* higher than about 1000 me./kg indicate excessive chloride or nitrate.

Specific shortages for K, Ca and Mg occur when their contents are lower than 200, 50 and 50 me./kg. Na is considered nonessential as a macroelement. The nutrient supply is balanced if the (*C—A*) content is normal. For grasses, grown under the various conditions of the experiments discussed, this is about 1000 me./kg. This quantity is necessary because the accompanying organic anions are required in this amount for good growth. The specific requirements for each of the organic anion species are not known. Nevertheless, a test on the nutritional status can be made with data on the macroelements only.

### 10.3 THE TEST

The purpose of nutritional tests is to evaluate whether the nutrition is adequate for good growth and, if not, to decide what measures should be taken to improve the nutrition for the next similar crop or for the same crop during subsequent growth.

Since the interrelations between elements are rather complex the test is summarized in a block diagram. A diagram, made for plants of perennial rye-grass and orchard grass in the vegetative stage, is given in figure 37 at the end of the paper. Decisions are given as tilted squares ( $\diamond$ ). The first square met contains (*C—A*) and has the exits  $\leq 900$ ,  $> 900$  but  $< 1100$ , and  $\geq 1100$ . This decision symbols should be read as



follows: follow the lines at the exits  $\leq 900$ ,  $> 900$  but  $< 1100$  or  $\geq 1100$  when the (C—A) content is lower than or equal to 900 me./kg, between 900 and 1100 me./kg or higher than or equal to 1100 me./kg, respectively. Instructions are given as blocks ( $\square$ ). Any instructions passed should be listed. If at any decision step the content is close to a value at the exit, one should follow both directions so that two lists of instructions are obtained. It will appear that, where both lists differ, a compromise is possible. In this way decisions with more than two alternatives are avoided.

### 10.3.1 Examples

The use of the diagram is illustrated by some examples given in table 12.

*Example 1* The (C—A) content of the plants without fertilizer is slightly lower than 900 and A is lower than 1000. Cl is higher than 250 so that the instruction *too much Cl* is given.  $\text{NO}_3$  is lower than 200 and the organic N lower than 2500 me./kg, so that N is obviously needed. The form of N to be applied depends on the K content. Here, K is below 600, and the instructions *apply N as nitrate* and *apply K without Cl* are given. Subsequently, Na excess and the specific shortages of P, Mg, S and Ca are tested. These tests do not lead to further instructions.

With the (C—A) content 850 the exit  $900 < (C-A) < 1100$  may also be followed. This only leads to the instruction *apply N*. A combination of both pathways indicates that N is definitely short, some K is required and the excess Cl is not serious.

Because of Ca nitrate application (C—A) dropped far below 900. A is below 1000. Since  $\text{NO}_3$  is higher than 200 and K lower than 400, the instruction *apply K* is passed. The P content of 70 indicates that the plants are at the verge of P shortage. The instruction: *too much Cl*, is now by-passed because of the nitrate application. With K nitrate (C—A) is slightly below 900,  $\text{NO}_3$  above 200 and K above 800, so that except for P no further instructions are given. The same result is obtained when the exit  $900 < (C-A) < 1100$  is used.

*Example 2* The (C—A) contents of the plants with 40 me. K nitrate and with 26 me. K nitrate + 14 me. Na nitrate are slightly higher than 1100. Whether the exit  $900 < (C-A) < 1100$  or the exit  $> 1100$  is used it is found that the plants needed N but not K and may have needed some additional P. The K content of the plants with 14 me. K nitrate + 26 me. Na nitrate is slightly lower than 500 so that, apart from N and P, these plants needed some K.

The path to be followed for the plants with 40 me. Na nitrate is outlined in detail. (C—A) is extremely high. Since K is much lower than 250, this is probably due to extreme K shortage. Hence the instruction *apply K*. Nitrate is 450 which indicates that some additional N may be needed. The boundary between the exits for nitrate is fixed at the high value of 400 because the increase in yield following K application results in an increased demand for N. Na is higher than 1000 and K is lower than 250 so that the instruction *too much Na* is given. Na is too much because it is likely that the uptake of K is considerably reduced by Na competition. According to the

TABLE 12 Composition of grass from pot experiments with different fertilizers. All values are in me./kg.  $\text{SO}_4$  is inorganic sulphate,  $\text{H}_2\text{PO}_4$  is total phosphate. The weight of the plant material at the application of the treatments was about 40 grams dry weight.

example	fertilizer	regrowth g d.m.	K	Na	Mg	Ca	Cl	$\text{H}_2\text{PO}_4$	$\text{SO}_4$	$\text{NO}_3$	C	A	organic	
													C-A	N
1	none	3	540	150	260	440	270	110	110	50	1390	540	850	1700
	40 me. $\text{KNO}_3$	9	1300	23	190	250	87	66	45	700	1760	900	860	2480
	40 me. $\text{Ca}(\text{NO}_3)_2$	7	310	190	360	700	150	70	40	700	1560	960	600	2550
2	40 me. $\text{KNO}_3$ + 0 me. $\text{NaNO}_3$	11	920	42	215	220	51	66	127	6	1400	250	1150	1440
	26 me. $\text{KNO}_3$ + 14 me. $\text{NaNO}_3$	11	710	230	210	210	37	63	120	6	1360	225	1140	1410
	14 me. $\text{KNO}_3$ + 26 me. $\text{NaNO}_3$	11	480	490	210	195	39	65	103	11	1375	220	1160	1420
	0 me. $\text{KNO}_3$ + 40 me. $\text{NaNO}_3$	7	108	1900	350	270	62	106	230	443	2630	840	1800	2030
3	50 me. $\text{Ca}(\text{NO}_3)_2$ + 3000 me. $\text{CaCO}_3$ (pH 7.1)	16	500	235	165	540	100	76	60	100	1440	335	1100	2450
	50 me. $(\text{NH}_4)_2\text{SO}_4$ + 3000 me. $\text{CaCO}_3$ (pH 7.0)	16	530	200	165	560	115	75	90	100	1460	380	1080	2480
	50 me. $\text{Ca}(\text{NO}_3)_2$ + 100 me. $\text{H}_2\text{SO}_4$ (pH 4.5)	18	520	155	200	420	96	71	60	100	1395	330	970	2180
	50 me. $(\text{NH}_4)_2\text{SO}_4$ + 100 me. $\text{H}_2\text{SO}_4$ (pH 4.3)	14	740	200	135	165	115	87	480	20	1340	700	640	2670
4	0 me. $\text{NH}_4\text{NO}_3$ + 0 me. $\text{K}$ + 0 me. $\text{Na}$ + 0 me. $\text{Cl}$	14	1000	60	200	300	280	176	120	0	1560	570	990	1600
	37.5 me. $\text{NH}_4\text{NO}_3$ + 0 me. $\text{K}$ + 0 me. $\text{Na}$ + 0 me. $\text{Cl}$	18	880	120	270	580	250	120	28	700	1850	1100	750	2850
	0 me. $\text{NH}_4\text{NO}_3$ + 30 me. $\text{K}$ + 30 me. $\text{Na}$ + 60 me. $\text{Cl}$	14	1300	200	170	280	1200	150	120	0	2050	1470	580	1800
37.5 me. $\text{NH}_4\text{NO}_3$ + 30 me. $\text{K}$ + 30 me. $\text{Na}$ + 60 me. $\text{Cl}$	19	1220	260	210	400	800	120	38	350	2090	1310	780	2800	

example 1: orchard grass, data of SAID (1959)

example 2: perennial ryegrass, data of VAN DEN BERGH, IBS, Wageningen (unpublished)

example 3: perennial ryegrass, data of DIJKSHOORN (1960)

example 4: perennial ryegrass, data of DIJKSHOORN (1958a)

diagram P in this case is adequate but the other treatments show that after K application P may be short. Different exit boundaries for P, Mg, S and Ca, depending on the K and N instructions are not given because the boundaries have been chosen well above the minimum level.

In the case that  $(C-A)$  is well above 1300 and K higher than 250 the plants are likely to suffer from lime-induced or iron chlorosis. It may be that application of  $NH_4$  restores the balance (compare CAIN, 1952).

*Example 3* concerns an experiment with soil treated with calcium carbonate ( $pH \approx 7$ ) or sulphuric acid ( $pH \approx 4.5$ ) and with  $(NH_4)_2SO_4$  or  $Ca(NO_3)_2$ . At  $pH 7$  there is no difference between  $NH_4$  and  $NO_3$  fertilization because of nitrification. There is some N shortage but K is about sufficient. The same holds for the nitrate application at  $pH 4.5$ . On the acid soil treated with  $NH_4$  the  $(C-A)$  content is much lower than 900 and the  $SO_4$  content much higher than 150, so that the instruction *too much  $SO_4$*  is given.  $NO_3$  is lower than 200 but organic N higher than 2500, so that the instruction *too much  $NH_4$*  is given. When  $(C-A)$  is not lower than normal a similar path with respect to nitrate and organic N does not give the instruction: *too much  $NH_4$* .

*Example 4* The test of the unfertilized plants yields only the instruction *apply N*. A test on Cl is unnecessary because the instruction *apply K* is not given and the  $(C-A)$  content is normal. The Cl content of 280 is therefore not too high.

With N application  $(C-A)$  is lower than 900 and A slightly higher than 1000 and the instructions *too much Cl* and *too much  $NO_3$*  are passed. Following the exit  $A \leq 1000$  the instruction: *too much  $NO_3$* , is not given because a subsequent decrease of the  $NO_3$  content at further growth is expected.

With K application (as  $KCl + NaCl$ ),  $(C-A)$  is much lower than 900 and A much higher than 1000. With Cl 1200 the instruction *too much Cl* is given. The exit boundaries for the Cl test are at a low value because under these conditions any reduction of the high A content is useful.  $NO_3$  is low and K more than sufficient.

With the N and K application N shortage is relieved but the low  $(C-A)$  and the high A contents are maintained.

*Example 5* Some plant compositions leading only to the instruction *macronutrition adequate* are given in table 10.

### 10.3.2 Differences between plants and crops

In section 8 it was shown that the yield differences resulting from different growth rates are much smaller for closed crops than for single plants, as long as more extreme shortages are absent. Therefore, inadequacy of nutrition, found by applying the present single plant test to closed crops does not necessarily imply that the crop yield is significantly depressed. This smaller yield response of closed crops is for the greater part taken into account by changing the figure 900 at the exits of  $(C-A)$  into 750. This boundary of 750 me./kg is based on experiments such as example 2, table 12, with densely planted grass in pot experiments.

#### 10.4 OTHER PLANT SPECIES

The normal (*C—A*) content of small grains in their vegetative stage is about 1200 me./kg. Apart from this they do not differ from grass. Therefore, the diagram for grass plants is practically suitable for small grains if the values at the exits of the (*C—A*) test are increased by 200.

The normal (*C—A*) content of buckwheat and beet is about 4500 me./kg. In this case a simple adjustment of the diagram for grass cannot be satisfactory. Moreover, beet and buckwheat differ from grass and from each other with respect to the relative uptake of the cations. Plantain did not show preference for any of the cations and a test diagram for plantain would be entirely different from the diagram for grass.

These examples suffice to show that the construction of test diagrams for other plant species requires similar basic information as given here for grass and small grains.

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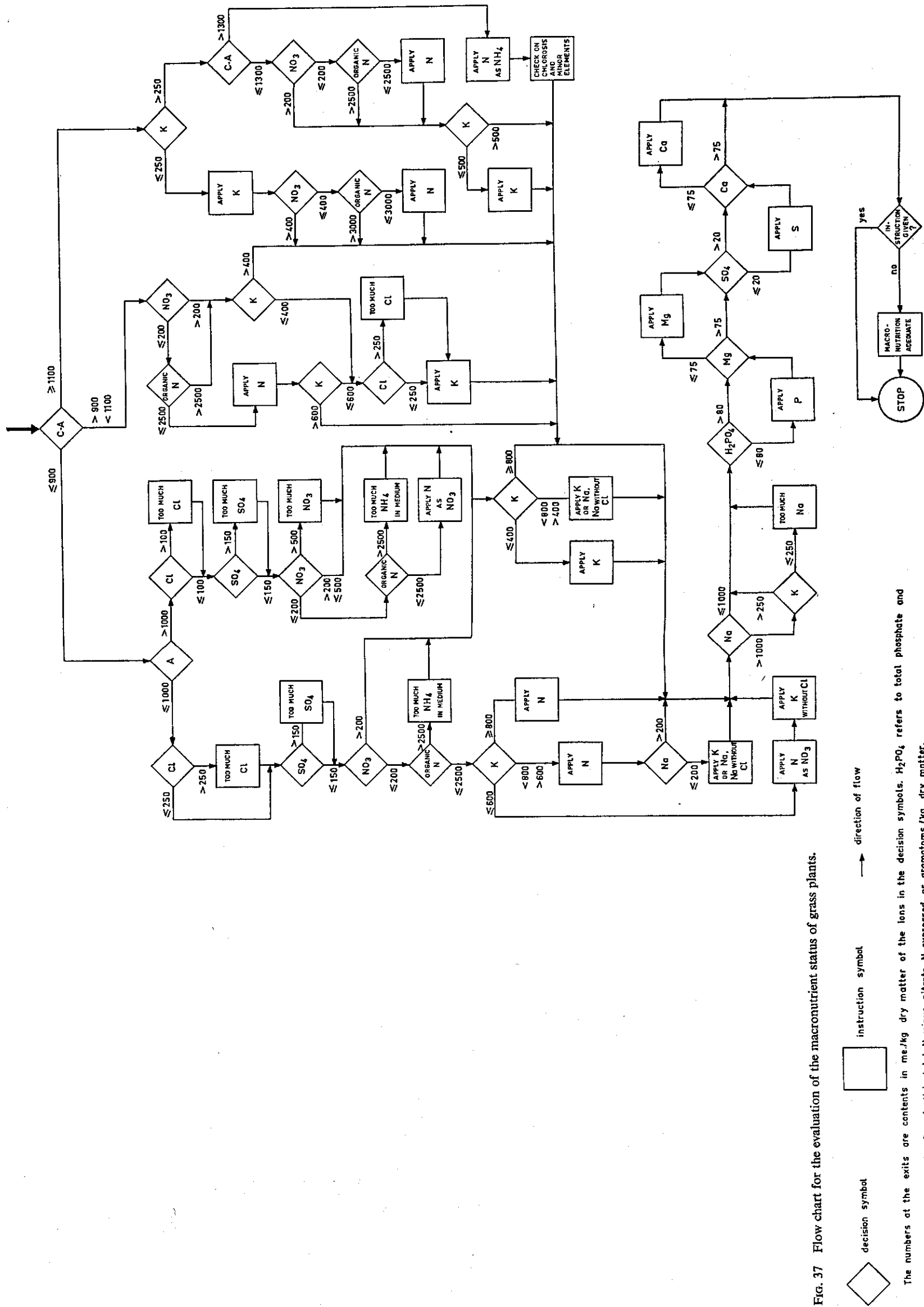
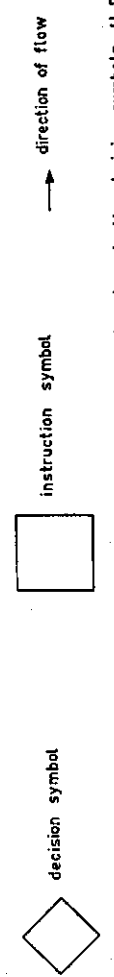


Fig. 37 Flow chart for the evaluation of the macronutrient status of grass plants.



The numbers at the exits are contents in me/kg dry matter of the ions in the decision symbols.  $H_2PO_4$  refers to total phosphate and  $SO_4$  to inorganic sulphate. Organic N is total N minus nitrate N expressed as gramatoms/kg dry matter.