

INTERRELATIONSHIPS BETWEEN POTASSIUM
AND MAGNESIUM ABSORPTION BY OATS
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1 INTRODUCTION

With practical importance to agriculture, one of the most interesting antagonisms in ion uptake by plants is that of potassium and magnesium. Magnesium deficiency is a rather old problem, which has already been studied over a long period of time (HUDIG and MEYER 1918, VAN ITALLIE 1937, SCHUFFELEN 1940, SMIT AND MULDER 1942). It has frequently been found to be associated with a disturbed balance between potassium and magnesium.

The classical approach toward studies on ion relationships made use of plants grown in cultural media over a relatively long period of time. More recent studies employ short-term cultures in which the selective accumulation and excretion mechanisms of ions are examined in excised roots, other plant parts, or individual cells. Both techniques will be used in the present study.

Inter-ionic influences on uptake under the "root-uptake" concept may be viewed within the framework of the commonly proposed carrier system for metabolic uptake. However, it must be stipulated in advance that not all ionic relationships found in carrier studies can be interpreted to be applicable to foliar tissues.

For instance, Ca and Mg show an inverse relationship in the leaf in many plants, but are reported to pass over different sites (EPSTEIN and LEGGETT 1954 and MOORE *et al.* 1961). This can be said also for Mg and K uptake. A strong reciprocal relationship between K and Mg in leaves has been found in many plants, but in long-term experiments by SCHARRER and MENGEL (1958), K was found not to compete with Mg absorption in the roots of intact corn and sunflower plants.

ZIMMERMANN (1947), JACOB (1955), SCHILLING (1957) and BAUMEISTER (1958) have presented reviews of studies on magnesium-potassium interactions. These reviews will be examined here insofar as they touch upon the uptake of Mg by plants as influenced by the ionic composition of the cultural medium.

The present review will deal with the absorption of Mg as influenced by cations and anions in general, and by certain ionic groups or individual ions. Special attention will be given to the effect of such relationships on crop yields and on the occurrence of Mg deficiency symptoms. Furthermore, absorption mechanisms, synergistic effects, and the protection of the integrity of selective ion transport systems, as studied in short-term experiments, will be reviewed.

1.1 MG AND K

It has been revealed by many investigators that, if the ratio of available K to available Mg in the soil is sufficiently high, chlorosis develops in plants due to Mg deficiency.

even when the growth medium has a relatively high content of available Mg (CAROLUS 1933, 1935, WALSH and CLARK 1945, WALSH and O'DONOHOE 1945, BOYNTON and COMPTON 1945, HUNTER 1946, MULDER 1950, SMITH and REUTHER 1954, SCHIJN 1955, FERRARI and SLUIJSMANS 1955, FISCHER 1956, MCCOLLOCH *et al.* 1957, MAZAEVA 1958, VAN DER MAREL *et al.* 1959, JAKOBSEN and STEENBJERG 1960, BROESHART and VAN SCHOUWENBURG 1961, HOFFMANN 1962).

Generally, Mg content is negatively correlated with K content in foliar tissues (stability of ion interaction direction in a tissue, EMMERT 1961). For instance, SCHREIBER (1949) working with wheat, barley, rye and oats found that, within one Mg series, the straw of all four cereals showed increasing K contents and decreasing Mg contents with increasing K applications.

Ion interactions are common to all plant parts, but are not necessarily of the same magnitude throughout the plant. SMITH *et al.* (1954) studied the effects of various N, K and Mg regimes on composition of leaves and fibrous roots of orange trees, and found that the interacting effects of the ions were often different for the two types of tissues investigated. GRUPPE (1958) reported that pot experiments with young apple trees showed normal development when the K/Mg ratio was less than unity. Maximum fruit yields required relatively high K applications, and the slight Mg deficiency thus produced had no harmful effects. A high supply of Mg at low K supplies, however, promoted the growth of wood and roots. Increasing supplies of K increased the concentrations of K and decreased those of Mg and Ca in the leaves, whereas the reverse was true with respect to the shoots.

SCHARRER and MENGE (1958) examined Mg uptake in intact maize and sunflower plants in a long-term water-culture experiment and noted that K did not compete with absorption of Mg by roots, and that the physiological K/Mg antagonism is restricted to green tissues, especially leaves. Decreased Mg uptake led to yield depressions as a result of impaired stalk development.

It has been indicated by some investigators that K depresses Mg uptake and that Mg depresses K uptake (reciprocity of interactions of ion pairs in absorption, EMMERT 1961). CAIN (1955) examined the uptake of Mg and K by apple trees from culture solutions and found that a high level of one often resulted in a reduced tissue concentration of the other. He also suggested that the effect can be ascribed to growth and translocation phenomena rather than to an antagonism operating during the intake phase.

Comparing the effect of ions on Mg uptake, PRINCE *et al.* (1947) reported that the most significant single factor influencing the Mg uptake of alfalfa plants is the quantity of available K and that, as the K supply decreases with repeated harvests of a crop like alfalfa, the Mg content of the plant increases, even when it is growing on a soil that is very deficient in Mg.

SHIVE (1916) studied the growth of wheat plants at 36 ratios of Ca : Mg : K at osmotic concentrations of 0.1, 1.75 and 4.0 atmospheres. He concluded that for any given set of salt proportions, the total concentration of the medium determines the

growth of plants. The values of the cation ratios Mg/K, Mg/Ca and Ca/K appeared to determine the growth of plants in many cases, but this relationship was not always clear for any single ratio and it generally required two of these ratio values to determine the physiological properties of the nutrient solutions with any given total concentration.

BOYNTON and ERICKSON (1954) reported that interveinal chlorosis and necrosis occurred in nursery beds of cacao seedlings because of Mg deficiency in soils of low Ca and high K content. Application of K inhibited Mg absorption, and Mg and K inhibited Ca absorption. Ca and Mg reduced the K concentration in the seedlings. K had a detrimental effect on tree stand, growth and Mg absorption on these soils with low base saturation and high exchangeable K.

For potatoes and sugar beets, HOVLAND and CALDWELL (1960) examined the relations between leaf-Mg contents and $\log \frac{\sqrt{a_{Mg}}}{a_K}$ values in soil solutions. This approach was suggested by WOODRUFF (1955), who found the net energy of the reaction involving replacement of Ca on soil colloids with K to be proportional to $\log \frac{\sqrt{a_{Ca}}}{a_K}$. HOVLAND and CALDWELL found that increases in $\log \frac{\sqrt{a_{Mg}}}{a_K}$ values of soil solutions coincided with increases in Mg contents of the crops examined.

There has been little research concerning the Mg uptake mechanism in relation to K in short-term experiments. CONWAY (1958) has investigated the Mg uptake mechanism by yeast and concluded that Mg ions under certain conditions can be actively transported in large amounts across the yeast-cell membrane by the physiological carrier of K ions. This transport occurs only when the Mg ion is the only inorganic cation present in the external fluid in appreciable concentration. The uptake of Mg in this way from a 0.2 molar solution is 50 per cent inhibited by 0.5 m-mole K ion per liter. The uptake curve descends more slowly starting from the 50% inhibition level than would be expected theoretically on the basis of the MICHAELIS-MENTEN kinetics and this may be due possibly to a small residual amount of Mg absorbed by a second mechanism of uptake of Mg ions operating at about pH 3.5 to 4.5, which mechanism is not inhibited by K ions.

It is evident from the above that little agreement exists as to the origin of antagonistic effects K and Mg might exert upon each other. Some workers contend that any antagonism between the two ions originates in green tissues, whereas others claim that competition for binding sites in roots must be responsible for disturbed balances between these ions.

1.2 MG AND CA

HASHIMOTO (1957) examined the Mg metabolism of soybean plants in water culture in relation to Ca and K, and found that excessive Ca concentrations (15 me. per liter) increased the K content in the alcohol-soluble fraction and in the acetic acid-soluble

fraction, especially in the former. Mg contents, however, were not affected. Mg-deficient plants contained little alcohol-soluble Mg. A high Ca rate with low Mg delayed the appearance of Mg deficiency symptoms and increased yield, possibly due to release of bound Mg. The Ca/Mg ratio for optimum yield varied between 3 and 9 by equivalency.

PFAFF and BUCHNER (1958) reported that Mg uptake is reduced in high acidic soils and enhanced by moderate applications of Ca and Mg, and when Mg supply is low, that the presence of sufficient lime appears to heighten the effectiveness of Mg present in the plant.

BUTIJN (1961) investigating Mg deficiency in apple and pear trees studied critical values of K/Mg ratios in leaves. He also found that Ca should account for a certain percentage of the sum of cations (K + Mg + Ca) in leaves in order to have healthy looking leaves.

JACOBY (1961) studied Mg uptake by citrus seedlings, as affected by the exchangeable Ca/Mg ratios in soils varying from 3 to 20. He mentioned that the critical ratios of exchangeable Ca/Mg in soils were found at 8 (deficient in Mg) and 4 (healthy).

KEY *et al.* (1962) undertook an experiment with soybeans and corn in soils with exchangeable Ca/Mg ratios varying from 50 to 0.2, and in sand-resin culture with Ca/Mg ratios of cation-resin varying from 50 to 0.02. In the soil culture, the Ca/Mg ratios had no significant effect on soybean yield, though growth tended to be poorer with a Ca/Mg ratio less than unity. In the sand-resin cultures, the Ca/Mg ratio had no effect when Ca exceeded Mg, and growth differences were associated with amounts rather than with the ratio of these ions. Poor growth resulted when the Ca/Mg ratio was < 1.

BOWER and WADLEIGH (1948), and WADLEIGH and BOWER (1950) studied the effect of Ca concentrations on Mg and K uptake with red kidney beans in water and resin cultures. The red kidney bean is a plant which easily shows Mg toxicity when the nutrient solution does not contain Ca. The Mg uptake in leaves was decreased with increasing Ca concentrations in the nutrient solution (1/8 to 4 me. per liter), while Mg contents in roots did not decrease appreciably.

WALKER and GROVER (1960) examined the effects of Ca and Mg on the growth of the common sunflower in water-culture solutions with Ca/Mg ratios varying from 1/3 to 1/25. They found that the vegetative yield dropped sharply with all decreases in this ratio. Mg contents were more useful than Ca contents in predicting yields.

COLLANDER (1941) showed an apparent identity of the absorption mechanisms of Ca and Sr, but Mg absorption did not follow the same pattern. He further indicated that the distribution of Mg between roots and shoots of many species of plants is not related in any consistent manner to that of Ca and Sr.

EPSTEIN and LEGGETT (1954) studied the absorption of alkaline-earth cations in short-term experiments with barley roots, and stressed that Mg is not competitive with Sr and by inference not with Ca, either. It could then be expected that Ca would not compete with Mg absorption, and, although it markedly interferes with the

absorption of Mg, the evidence suggests that this interference is not in the nature of competition for identical sites according to EPSTEIN's discussion (1962).

MOORE *et al.* (1961) studied the Mg uptake with excised barley roots in a short-term experiment. They mentioned that, although Ca was very effective in blocking Mg absorption, the blocking action was not quite complete. Increasing the Mg concentration in the presence of Ca did not overcome the blocking action of Ca on Mg uptake. Even at a ratio as high as 20 me. Mg per liter to 1 me. Ca per liter, the blocking action was still quite pronounced. When two ions mutually compete, each ion has a depressing effect on the metabolic absorption of the other. Therefore, it is impossible to explain the effect of Ca on Mg as being simply a mutual competition for the same binding site. The action of Ca may at some point be different from that at the binding site. The authors concluded that Ca may influence Mg uptake by altering the structural configuration of the surface groups of cells in such a way as to markedly change their chemical and physical properties.

1.3 MG AND H

In the Netherlands, the first observations made on the disorder later called Mg deficiency were made by HUDIG and MEYER (1918), who diagnosed the phenomenon as caused by an excess of H ions.

SCHUFFELEN (1940) showed with artificial soils varying in quantities of exchangeable cations that high levels of exchangeable H induced mottling in oats. One possible treatment for rectifying the disorder was raising the pH of the growth medium. It was, however, made clear that other ions besides Mg and H also played important roles in causing or preventing the occurrence of mottling.

FERRARI and SLUIJSMANS (1955) also investigated the effect of pH on the mottling and Mg content of oats at different fertilizer treatments and at different levels of Mg content in soils. They mentioned that the significance of the pH for the Mg supply of the plant is probably of an inhibitory nature, mainly associated with root development.

Contrary to many other workers, SCHACHTSCHABEL (1956) found no direct correlation between soil pH and Mg deficiency symptoms for potatoes.

EPSTEIN (1961, 1962) and RAINS *et al.* (1962) mentioned that pH effects on cation uptake under physiological conditions, which include the presence of Ca, are less significant than some investigations seem to suggest. HOAGLAND and BROYER (1940) likewise found only a small effect of external pH on the uptake of ions.

On the other hand, MOORE *et al.* (1961) studying the effect of pH on Mg uptake with excised barley roots, found the shape of the pH-Mg uptake curve to be quite similar to that for K. Mg uptake increased sharply with pH increasing from 3.5 to 6 in solution.

CONWAY (1958) investigated the effect of pH on Mg uptake by yeast, and found that

the Mg uptake is extremely sensitive to the presence of K ions and also to that of H ions, there being a marked sensitivity to the pH between 5.5 and 7.0 in Mg uptake. This author postulates two mechanisms of Mg uptake: one operating between pH 3.5 and 4.5 is not sensitive to H ions; the other operating above pH 4.5 is inhibited at the lower range by H ions.

It appears that the magnitude at which H ions influence the uptake of Mg is dependent on experimental conditions. In many investigations, no clear distinction is made between direct influences of H ions and secondary effects of pH differences on Mg uptake.

1.4 K + Mg, K + Mg + Ca, etc.

A primary change in content of a single ion in plants influences concurrently the contents of other ions. Many workers who studied the ionic composition of plants detected a certain constancy in concentration of total cations. (McCALLA and WOODFORD 1938, BEAR and PRINCE 1945, LUCAS and SCARSETH 1947, WALLACE *et al.* 1948, SCHUBERT 1949, MEHLICH 1949, WOODBRIDGE 1955, ICHIKAWA 1958). In addition, it was found that the ratio cations to anions in plants tends to be constant (VAN ITALLIE 1934, BEAR 1950, DIJKSHOORN 1957a, 1957b, 1958a, 1958b).

CALMÉS (1959) examined Mg and K contents in leaf blades of maize, and found that when N or P was withheld, leaf K was high and Mg low, whereas the reverse applied where K was withheld. In each of these cases the sum of K and Mg remained fairly constant. He suggested that K and Mg may be important in maintaining ionic equilibrium.

OLSEN (1942) studied K, Mg and Ca uptake by several species of plants and found that for most of the plants used, the sum of the three cations per gram of dry leaves was constant in the same K concentration series. He also found that the sum of cations was constant in leaves when K was varied at constant Mg and Ca concentrations in solution.

CAIN (1948), however, noted that the sum of cations in apple leaves did not remain constant and increased with increasing N applications.

HUNTER (1949), in a pot experiment, examined the effect of varying ratios of exchangeable Ca/Mg upon the growth of alfalfa and its contents of P, Mg, Ca, K, N and lignin. He reported that the percentages of Ca, Mg and K in alfalfa varied over wide ranges with varying Ca/Mg ratios, but that the sum of equivalents of the three cations was constant.

1.5 Mg and N

Experimental evidences show that Mg enhances NO_3^- uptake and NO_3^- enhances Mg uptake (HOBLYN 1940, OLSEN and BLEDSOE 1942, BOYNTON and COMPTON 1944, CAIN

1953, SCHACHTSCHABEL 1956, PFAFF and BUCHNER 1958, JAKOBSEN 1960, HOLMES 1962).

OBENSHAINE (1944) showed in sand cultures with corn that, as the supplies of N were increased, the tissues contained more Mg, and that increased supplies of K induced increase of P in sap and decreases of both Mg and Ca in sap and tissue.

MULDER (1956) examined the relationship between Mg and NH₄ or NO₃ in soil culture with cereals and showed that the uptake of small amounts of Mg was directly stimulated by NO₃ ions. Potatoes in the field developed more severe symptoms of Mg deficiency in presence of 80 kg MgO/ha without added N than with an application of 140 kg N/ha in the form of ammonium nitrate limestone without Mg. Ammonium sulfate had a detrimental effect upon yield. The beneficial effect of nitrate on Mg uptake was attributed to a decrease of H ions within the cytoplasm after assimilation of the nitrate.

IZAWA *et al.* (1957) found with rice plants that increased K supply caused more Mg to be absorbed in the presence of NO₃. No change was found with application of (NH₄)₂SO₄.

MULDER (1958) also carried out a pot experiment with wheat and oats treated with various levels of N fertilizers with or without MgSO₄ added. The uptake of Mg was depressed and deficiency symptoms developed when (NH₄)₂SO₄ was applied. Mg uptake increased with NaNO₃, Ca(NO₃)₂ and NH₄NO₃ applications and Mg deficiency symptoms decreased in this order. In field experiments with wheat and potatoes, Mg uptake and yield were greatly increased by Ca(NO₃)₂ (especially in wheat) and by NH₄NO₃ and lime applications, and were markedly depressed by application of (NH₄)₂SO₄, possibly due to increased leaching of Mg as a result of higher acidity levels. Healthy plants on Mg-poor light-textured soils of high acidity may be produced when NO₃ fertilizers are applied.

1.6 MG AND P

TAKAHASHI and YOSHIDA (1958) noted that the supply of P influenced the total Mg content of the tobacco plant. In the low-Mg treatment, chlorophyll-magnesium decreased and Mg deficiency symptoms increased with increasing P supplies. The authors advanced the hypothesis that Mg is necessary for the metabolism of absorbed P and that, when Mg supply is low, Mg needed for chlorophyll formation is expended on P metabolism, resulting in Mg deficiency.

SEO and ICHIKAWA (1958) studying the relationship between Mg and P uptake by tomato in water cultures, observed that at medium Mg levels, contents of Mg in tomato leaves were increased by increasing P levels, but that such increases were absent at the low-Mg level, and that Mg deficiency symptoms were promoted by high P levels. Conversely, at medium P levels, increasing Mg supply led to higher P contents, whereas at low P levels such increases were absent. In general, these authors found positive relationships between Mg and P contents.

HELMY *et al.* (1960), however, found P contents in cotton to be suppressed by high Mg levels. BROESHART and VAN SCHOUWENBURG (1961) reported a similar finding for oats.

1.7 MG AND S

WALSH and CLARKE (1945) noted that a low level of S nutrition retarded development of Mg deficiency symptoms by enhancing Mg uptake in tomatoes.

1.8 ION ABSORPTION AND ION MOBILITIES

VAN ITALLIE (1937, 1938) pointed out that for Italian rye grass replacing or competing abilities of ions are in the order of $K > Na > Mg > Ca$. However, as indicated by PIERRE (1943), the position of Na in the cation competition series seems to vary considerably, possibly because of the wide differences in the capacities of various plants to absorb Na from the medium. CAROLUS' work (1935) with potatoes, a low-Na plant, shows, for example, that Na depresses K absorption less than does Mg.

COLLANDER (1941) and later on many others showed that cation replacement was more marked among closely related cations such as Ca and Sr, or K and Rb, than between divalent and monovalent cations.

LUNDEGÅRDH (1940, 1951) showed that roots contain much Ca, while K contents are lower in roots than in leaves. The accumulation of Ca in roots is explained by the low speed of migration of this ion within plants. In comparison, the monovalent K ion moves more quickly. He mentioned that the parallelism between the speed of migration of ions in colloidal media and their distribution in the plant was confirmed by an investigation of BURSTRÖM (1934), as far as cations are concerned.

According to MIDDLETON and RUSSELL (1958) and RUSSELL (1962), the order in which ions compete for entry into the first phase of absorption is the inverse of that in which they are subsequently actively transported. Di- and polyvalent ions compete successfully with monovalent ions in the first step, but their subsequent active accumulation is slower, although with the passage of sufficient time even the largest and slowest ones break through.

ROBERTSON (1958) also, pointed out that in general, ions may be expected to show more mobility in the plant if less charged or less hydrated (e.g. $K^+ > Na^+ > Li^+$), although the order of ion mobilities in living systems is variable.

1.9 SYNERGISTIC EFFECTS OF IONS ON EACH OTHER'S ABSORPTION

Li, Ca, Mg and other divalent and trivalent cations accelerate the rate of absorption of K, Rb, Br, SO_4 and PO_4 (VIETS 1944, JACOBSON *et al.* 1950, OVERSTREET *et al.* 1952, FAWZY *et al.* 1954, TANADA 1955, NIELSEN and OVERSTREET 1955, LEGGETT and

EPSTEIN 1956, KAHN and HANSON 1957, MIDDLETON and RUSSELL 1958, GROBLER 1959, EPSTEIN 1960, JACOBSON *et al.* 1960, JACOBSON *et al.* 1961).

As mentioned by EPSTEIN (1962), when at low pH values absorption of cations is higher in the presence than in the absence of Ca, the effect of Ca is in his opinion not so much in the nature of a straightforward stimulation but rather a reversal of the toxic effect of H ions. Ca concentrations as low as 0.5 m-mole are sufficient to overcome these adverse effects of H ions. However, positive effects on absorption of cations by Ca at pH 5 and above, and increasing with increasing concentrations of Ca up to very high values (10 m-moles and more) must be looked upon as real stimulations, apart from any H-ion effect, and the same applies to positive effects of Ca on the rate of absorption of anions. These synergistic effects observed by VIETS and others are slight or non-existent at a Ca concentration of 0.5 m-mole, and require concentrations twenty to fifty times this value for saturation. Mg was found to be equally effective or nearly so (Viets 1944, EPSTEIN 1961, JACOBSON *et al.* 1961). However, Mg can not substitute for Ca in overcoming the deleterious effects of H ions.

OVERSTREET *et al.* (1952) suggested that divalent ions stimulate the entry of monovalent ions by participating in the mechanisms whereby the monovalent ion Rb is bound within cells.

MIDDLETON and RUSSELL (1958) compared this stimulatory effect with the type of interaction between mono- and divalent cations which can occur in simple cation exchange columns. By virtue of its greater ionic size, the divalent ion competes successfully for sites at the initial point of entry, thus displacing monovalent ions from such sites or preventing their retention, so that their movement down the column is accelerated. They pointed out that OVERSTREET's hypothesis cannot easily be applied to explain the same stimulatory effect of trivalent cations on monovalent cations.

On the other hand, HELMY *et al.* (1963) tried to explain the stimulatory action of Ca by implying that the initial cation content of roots is important in determining cation uptake. Thus, when the initial content ratio of Ca/K in roots is high, the roots do not absorb Ca without absorbing K first, and K and Ca may take part in forming one carrier complex (Ca-K-R). They mentioned that their observations cannot be explained by the hypothesis of MIDDLETON and RUSSELL (1958) that Ca affects the absorption of K by simple considerations of exchange processes in resin columns.

JACOBSON *et al.* (1960) in attempting to explain the stimulation effect of Ca on K, Rb and Cs uptake reasoned that the presence of Ca in the solution creates a barrier, probably at the cell surface, and that this barrier which is particularly effective in blocking Li and H, determines the relative quantities of cations reaching the absorption site. However, WAISEL (1963) showed that the decrease in Li absorption caused by Ca is due to an effect on the metabolic absorption process (competition on the carrier) and not to a decreased access of Li ions to the sites of the absorption process. The latter might result, if Ca would form or would induce the formation of some kind of mechanical screen resulting in an increased resistance of cell membranes to diffusion of Li ions, according to the concept put forth by JACOBSON *et al.* (1960).

1.10 INTEGRITY OF SELECTIVE ION UPTAKE

It has been found by several investigators that Ca is essential for the integrity of selective cation (or anion) transport mechanisms by plant cells (JACOBSON *et al.* 1961, EPSTEIN 1961). In the absence of Ca, the selectivity in absorption of K and Na by barley roots quickly breaks down, the impairment being evident within minutes from the start of the experiment. This derangement is only partially reversed by subsequent addition of Ca to the solution.

Certain other divalent cations (Sr, La, Mn, Al etc.) were more or less effective in maintaining the integrity of the selective transport mechanisms, but Mg is ineffective according to EPSTEIN (1961).

JACOBSON *et al.* (1961) found that, when Ca is absent from the solution or present in very low concentrations, e.g. less than 0.05 m-mole per liter, the selective absorption mechanism for K uptake by barley roots is deranged. However, the Ca requirement for the integrity of selective transport of K and Na is completely satisfied by a rather low concentration of 0.5 m-mole Ca with barley roots, while the synergistic effect of Ca needs a higher concentration of 10 to 25 m-moles Ca, and is slight or non-existent at a concentration of 0.5 m-mole per liter with barley roots (EPSTEIN 1961, VIETS 1944, OVERSTREET *et al.* 1952).

It is clear from the above that ion interactions in plant parts are influenced by many factors, the combined effects of which cannot easily be studied in one experiment. In the present investigation, an attempt is being made:

1. to elucidate in a long-term water-culture experiment the relationships between the composition of the external medium and the nutrient status of different plant parts of oats.
2. to study in short-term experiments the relationship between ion uptake and external medium, using intact oat plants.
3. to relate the results obtained in both types of experiments, with special attention directed to K and Mg uptake as a function of variations in the K/Mg ratio in the external medium.

2 LONG-TERM WATER-CULTURE EXPERIMENT

2.1 TECHNIQUES OF WATER-CULTURE EXPERIMENTS

The main object of the present study was to investigate the direct relationship between Mg uptake by oats and the composition of the ambient solution. Any soil factors influencing this relationship had to be eliminated. Hence, a water-culture technique was employed. In the following, some important points regarding water-culture experiments will be discussed.

2.1.1 *Stirring and concentration of solution*

In order to investigate relationships as the one under investigation it is important to keep cultural conditions constant for all treatments. Aside from uniformity in temperature, light, moisture, solution volume, tools, etc., care should also be taken to minimize for each treatment any changes in concentration and pH of cultural solutions.

OLSEN (1950, 1953) studied the significance of concentration of nutrient solution and stirring of solution upon the rate of ion absorption by rye and kale in a water-culture experiment. He concluded that except for very low concentrations, i.e. below 0.003 me. per liter in the case of NO_3 and PO_4 , ion absorption is independent of ion concentration in solution, provided the solution is stirred during the experiment. If the solution remains unstirred, the plant will first absorb the ions from that part of the solution nearest to the roots, resulting in a considerable gradient in concentration of ions in solution. Such a gradient is eliminated by diffusion but, as is well known, this is a slow process. The greater the gradient in concentration, the stronger however will be the stream of ions diffusing toward the root. Therefore, plants in unstirred solutions absorb relatively greater amounts of ions from solutions with higher concentrations.

In solutions containing 8 me. or more of NO_3 per liter, stirring of the solution by aeration did not appreciably influence the rate of ion uptake by rye plants. In a solution of less than 8 me. NO_3 per liter, the absorption rate was considerably increased by aeration, and the difference between absorption rates in aerated and unaerated solutions increased with decreasing concentrations in solution. At a concentration of 0.0015 me. NO_3 per liter, the rate of uptake was increased twentyfold by aeration.

Another reason for poor reproducibility of plant growth in unaerated solutions lies in the fact that the pH of the solution does not remain constant and changes first in the immediate vicinity of the roots where it gives rise to a poorly defined pH value which, in turn, may cause differences in rate of ion absorption.

At sufficiently high concentrations in both single-salt solutions and composite nutrient solutions, the number of ions absorbed per unit of time is constant. In the

latter case, however, constancy of absorption may only hold insofar as concentration ratios of the ions in solution do not change significantly during the absorption period. The rate at which the individual cations or anions are absorbed from a composite solution of moderate strength is determined by the ratio between these ion concentrations, but not by their absolute concentration in the solution. The total absorption per unit time of cation or anion equivalents is constant.

BARBER (1962) discussed the influence of diffusion and mass-flow on the uptake of nutrients in soil. He mentioned that the concentration gradient between root surface and surrounding soil, as established for a specific ion, will depend on several factors. Among them, there are:

1. the rate of diffusion of the ions to the root surface, and
2. the rate of movement of the ions to the root surface by "mass-flow".

Under natural conditions, most of the time plant roots will be in an environment where diffusion and mass-flow are governing uptake.

In the present long-term water-culture experiment, the large number of pots prevented the use of stirring or aeration devices. In order to minimize the disadvantages associated with unstirred media, the solutions were changed every three days. Nevertheless, the results obtained for the lower concentrations (tables 1 and 4) may differ from those found in experiments in which the solutions are stirred, as pointed out by OLSEN (1950, 1953).

2.1.2 Solution composition

For practical purposes, three cases may be considered in designing an experiment investigating the influence of various K concentrations in the cultural medium on the uptake of Mg by plants. Use can be made of

1. a constant Mg concentration with varying K concentrations,
2. a constant K concentration with varying Mg concentrations, and
3. a constant (Mg + K) concentration with varying K/Mg ratios.

In case (1), the ratios of all ions, except K, to the Mg ion can be kept constant, while the ratios of all ions to the K ion will vary. In addition to the variation of the K/Mg ratio in solution, the effects of the variation in ratio of all other ions to the K ion upon the uptake of Mg will have to be taken into account. Furthermore, anion concentrations will vary, and the effect of these variations upon Mg uptake should be considered also. An example of an experiment employing this design is that described by OLSEN (1942).

In case (2), the same considerations apply. The effects of varying ratios of all ions to the Mg ion and of varying anion concentrations upon Mg uptake have to be considered. An example is the work of BROESHART and VAN SCHOUWENBURG (1961) with oats.

In case (3), the effects of varying ratios of all ions to the Mg ion and to the K ion upon Mg uptake have to be taken into consideration. In this case, the concentrations of (K + Mg), the sum of cations, each anion and the sum of anions can be kept

constant. Consequently, the electric potential of roots can also be held more constant in this design compared with the other two. The values of ionic strength will vary little in series with similar concentrations even though individual concentrations of K and Mg will be different in each treatment (LAGERWERFF 1961, HELMY *et al.* 1963). An example is the work by BROESHART (1962) with oats. A design of this nature was used in the present experiment.

If in such a design, the ratios of other ions to Mg are taken as factors in the first series, and the ratios of other ions to K as factors in the second series, then the effects of single and combined factors of both series upon the uptake of Mg can be compared. For the single factors of the first series, it can be assumed that one factor, the K/Mg ratio, will exert the largest influence on Mg uptake. Another factor, the Ca/Mg ratio, can also be expected to be of appreciable importance (PRINCE *et al.* 1947, also see Chapter 1).

For instance, in cases of Mg deficiency in citrus PRATT *et al.* (1957) reported ratios of available K to Mg in soils to lie between 0.3 and 0.7 and JACOBY (1961) reported Ca/Mg ratios between 4 and 8. This may mean that K is approximately 10 times as effective as Ca in depressing Mg uptake by citrus.

The values of the single factors in the second series vary only by a factor of 2. For instance, the K/Ca ratio in solution changes from 0.5 to 0.99 with K/Mg ratios changing from 1 to 79 (Table 3). These effects of single factors in the second series on Mg uptake may be much smaller than the effect of the factor K/Mg ratio in the first series, considering the characteristics of K uptake by plants.

The overall effect of the combined factors on the uptake of Mg can be expected to be rather complicated, but only of secondary importance in comparison with that of the factor K/Mg ratio.

2.2 EXPERIMENTAL METHODS

2.2.1 Cultural solutions

The design selected was a complete factorial experiment having 7 K/Mg levels, 3 pH levels and 4 levels of concentration in the culture solution. Each treatment was duplicated, resulting in

$$7 \times 3 \times 4 \times 2 = 168 \text{ pots}$$

$$(\text{K/Mg}) \ (\text{pH}) \ (\text{conc}) \ (\text{reps})$$

The compositions of the nutrient solutions are shown in table 1. Chemicals used to prepare the solutions were the following: KNO_3 , K_2SO_4 , $\text{Mg}(\text{NO}_3)_2$, $\text{Ca}(\text{NO}_3)_2$, H_3PO_4 , KH_2PO_4 , K_2HPO_4 , and Ferric-EDTA. All chemicals were of C.P. grade.

(K + Mg), Ca, and anion concentrations were held constant in each pH and concentration series, except for slight differences in SO_4 concentration in each pH series. The pH levels of nutrient solutions were obtained with varying mixtures of phosphoric acid and potassium phosphates.

Varying the K/Mg ratio in the first series of factors affecting the Mg uptake, as

TABLE 1. Design of nutrient solutions

Variables	pH	K/Mg	Concentration (per liter)						
	3 levels	7 levels	at each pH level				pH 4	pH 5	pH 6
	by normality	K + Mg me.	Ca me.	NO ₃ me.	P m-mole	Fe m-mole	SO ₄ me.	SO ₄ me.	SO ₄ me.
Values of variables	4	79	2.5	2.5	4	0.25	0.0125	0.76	0.74
	5	39	5	5	8	0.5	0.025	1.52	1.48
	6	19	10	10	16	1.0	0.05	3.04	2.96
	9	20	20	32	2.0	0.10	6.08	5.92	5.60
	4								
	2								
	1								

mentioned under 2.1.2, changed the ratios Ca/Mg, Fe/Mg, NO₃/Mg, P/Mg and SO₄/Mg. Varying this ratio in the second series of factors, affecting Mg uptake, changed the ratios K/Ca, K/Fe, K/NO₃, K/P and K/SO₄. These varying ratios are shown in table 2.

TABLE 2. Ratios of elements to Mg and K in nutrient solutions

RATIOS, OTHER ELEMENTS TO MG					
K/Mg	Ca/Mg	Fe/Mg	NO ₃ /Mg	P/Mg	SO ₄ /Mg
					pH4 pH5 pH6
79	80	0.96	128	8	24.4 23.6 22.4
39	40	0.48	64	4	12.2 11.8 11.2
19	20	0.24	32	2	6.1 5.9 5.6
9	10	0.12	16	1	3.05 2.95 2.8
4	5	0.060	8	0.5	1.52 1.47 1.4
2	3	0.037	5	0.3	0.95 0.92 0.87
1	2	0.025	3.3	0.2	0.63 0.61 0.58

RATIOS, K TO OTHER ELEMENTS					
K/Mg	K/Ca	K/Fe	K/NO ₃	K/P	K/SO ₄
					pH4 pH5 pH6
79	0.99	82.3	0.62	9.88	3.24 3.35 3.53
39	0.98	81.3	0.61	9.75	3.20 3.31 3.48
19	0.95	79.2	0.59	9.50	3.11 3.22 3.39
9	0.90	75.0	0.56	9.00	2.95 3.05 3.21
4	0.80	66.7	0.50	8.00	2.62 2.71 2.86
2	0.67	56.7	0.43	6.80	2.23 2.31 2.43
1	0.50	43.3	0.33	5.20	1.70 1.76 1.86

Note: Ratios are by equivalency except P by molarity

TABLE 3. Ratios and concentrations of K and Mg in pH 4, 5 and 6 nutrient solutions

K/Mg by normality	(K + Mg) me.							
	2.5		5		10		20	
	K	Mg	K	Mg	K	Mg	K	Mg
79	2.47	0.03	4.94	0.06	9.88	0.12	19.76	0.24
39	2.44	0.06	4.87	0.13	9.75	0.25	19.50	0.50
19	2.37	0.13	4.75	0.25	9.50	0.50	19.00	1.00
9	2.25	0.25	4.50	0.50	9.00	1.00	18.00	2.00
4	2.00	0.50	4.00	1.00	8.00	2.00	16.00	4.00
2	1.67	0.83	3.34	1.66	6.68	3.32	13.36	6.64
1	1.25	1.25	2.50	2.50	5.00	5.00	10.00	10.00

As indicated in table 3, the Mg concentration varied by a factor of 40 in the same concentration series, whereas the K concentration varied only by a factor of 2. These variations produced values of K/Mg ratio ranging from 79 to 1, with constant concentrations of (K + Mg).

2.2.2 Plant material

The plant used was oats (*Avena sativa*, variety Marne). Containers used were 2.5-liter glass pots, diameter 12 cm, height 22 cm, cylindrical; the pots were placed in white wooden boxes. Per container, 8 plants were used. The pots were filled with 2.4 liters of nutrient solution. The solution was changed twice a week.

The cultural period lasted from July 25 till August 24, 1961. Prior to this period the seeds were sown in sand on July 20, and were watered daily. On August 3, 11, and 24, observations were made of general growing conditions and of Mg deficiency on leaves.

On August 22 and 23, portions of leaves near the tips (1 × 4 cm) were sampled for chlorophyll determinations. The assumption was made that these leaf portions were representative of whole leaves in determinations of chlorophyll magnesium.

On the 30th day following transplanting, all plants were harvested, and dried at 80°C. Roots and tops were analyzed separately for K, Mg, Ca, N and P. The chemical analyses were carried out according to methods, developed by SCHUFFELEN *et al.* (1961). K and Ca were determined by flame photometric methods, Mg and P were determined colorimetrically, employing the thiazole-yellow and molybdenum-blue methods, respectively.

N determinations were made with a modified micro-Kjeldahl method. Acetone extracts of leaves were analyzed colorimetrically for chlorophyll (ARNON 1949).

The contents of elements were expressed as me. per 100 g of dry matter, except for phosphates which were expressed as m-mole P. Mg in chlorophyll (Ch-Mg) was calculated on the basis of an average of 2.70% Mg in chlorophyll a and b, and ex-

pressed as Ch-Mg, me. per 1000 g of fresh leaves. The estimates thus obtained correspond roughly to me. Ch-Mg per 100 g dry matter.

Yield was expressed as grams of dry matter per pot for both tops and roots.

2.3 EXPERIMENTAL RESULTS

2.3.1 *Observations on general appearance and Mg deficiency symptoms*

After transplanting the seedlings to nutrient solutions, observations were made once a week for Mg deficiency as revealed by mottling in leaves, and for general growth of tops and roots. Already one week after transplanting, mottling appeared in the treatments with higher K/Mg ratios in solution (19 to 79). In each pH and concentration series, the phenomenon was slightly visible for the K/Mg ratio 9, and was absent for K/Mg ratios ranging from 1 to 4, as shown in table 4. No effects of pH

TABLE 4. Observations on Mg deficiency as revealed by mottling in leaves at all pH levels employed

K/Mg in solution	(K + Mg) me. conc. of solution			
	2.5	5	10	20
79	++++	++++	+++	+++
39	++	++	++	++
19	++	++	++	++
9	+	+	+	+
4	0	0	0	0
2	0	0	0	0
1	0	0	0	0

Legend for degree of Mg deficiency symptoms:

- +++ *heaviest, yellowish*
- ++ *rather heavy, yellowish*
- ++ *clearly visible*
- + *slightly visible*
- 0 *healthy*

Observations made on Aug. 3, 11 and 24, 1961.

Slight differences in severity of symptoms were found at different dates of observation and among different pH solution series.

and solution concentration on severity of mottling could be detected within the range employed. As the experiment progressed the degree of mottling became slightly more severe in the higher K/Mg ratio series and slightly less severe in the lower K/Mg ratio series.

Growth conditions were generally more favorable in the lower K/Mg ratio and pH 5 and 6 series, and taller plants were found in the series with higher concentrations. The concentration of 10 me. (K + Mg) in solution seemed to be the optimum medium for growth.

Better developed root systems with more hair roots of a light brown color were

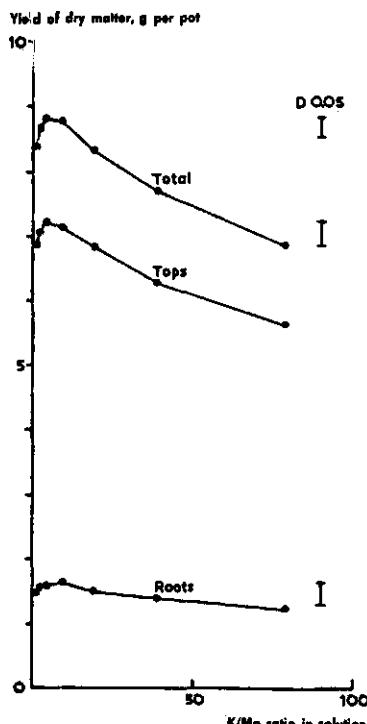


Fig. 1.

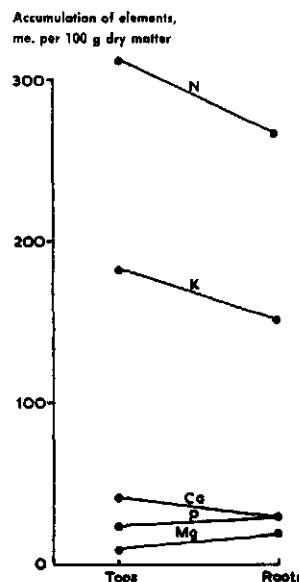


Fig. 2.

FIG. 1. Effect of K/Mg ratio in solution on yield of dry matter

FIG. 2. Nutrient contents in tops and roots, me. (P in m-moles) per 100 g. dry matter

FIG. 3. Nutrient contents in tops and roots at different pH levels

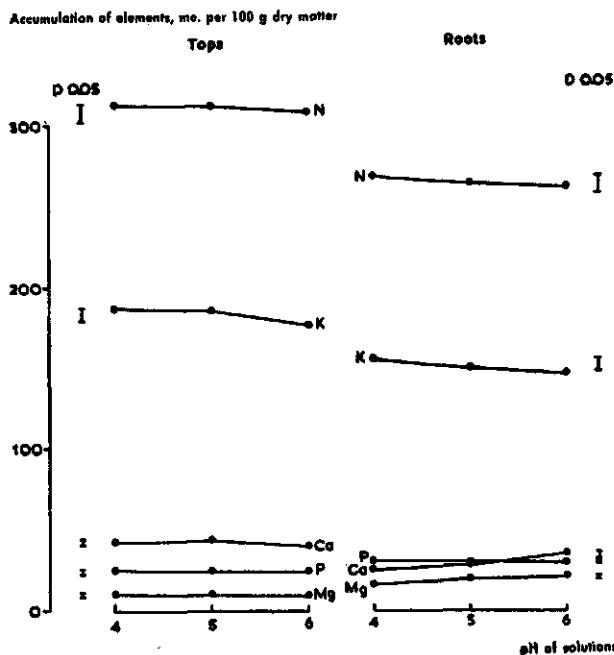


Fig. 3.

TABLE 5. Results (F values) of analyses of variance of yield of dry matter and absorbed nutrients in oats

Source of variation	Yield	Tops/ Roots	K	Mg	Ch-Mg	Ca	N
pH	66.17**	5.34**	11.91**	19.07**	38.10**	10.14**	1.85
K/Mg concentration	44.11**	< 1	62.37**	319.40**	29.79**	5.77**	2.42*
Pl. parts (tops; roots)	85.73**	56.75**	30.57**	26.16**	3.46**	122.65**	42.57**
pH × Pl. part	16867.64**	—	419.76**	763.59**	—	303.59**	447.63*
K/Mg × Pl. part	25.73**	—	1.12	23.46**	—	23.73**	< 1
conc. × Pl. part	17.13**	—	2.03	13.30**	—	5.95**	3.22*
pH × conc.	75.95**	—	3.59*	12.42**	—	120.54**	5.41*
pH × K/Mg	1.83*	1.24	< 1	< 1	9.10**	< 1	1.19
pH × K/Mg × conc.	4.85**	1.73	2.21*	2.92**	1.46	6.81**	1.76
K/Mg × conc.	3.67**	< 1	2.82**	2.21**	< 1	2.89**	1.01
pH × K/Mg × Pl. part	< 1	—	1.07	1.06	—	< 1	< 1
pH × conc. × Pl. part	2.42*	—	1.69	3.69**	—	7.94**	< 1
K/Mg × conc. × Pl. part	1.61	—	1.28	3.40**	—	2.57**	< 1
pH × K/Mg × conc. × Pl. part	1.83**	1.09	1.90**	1.37	1.08	< 1	< 1
C.V. (%)	8.75	7.98	8.73	19.91	9.72	17.12	6.99

Ch-Mg = Chlorophyll-Mg, Mg = Total Mg

C.V. = coefficient of variation = $\frac{s}{\bar{x}} \times 100\%$ (s = standard deviation)

found in the pH 5 and 6 series, whereas smaller and white-colored root systems prevailed in the pH 4 series. The roots in solutions of higher concentrations were shorter than those found in more dilute solutions (Photographs 1 to 6; see pages 93-95).

In the photographs 1 to 6, concentration in solution is expressed in moles of $\text{PO}_4 \times 10^{-4}$ instead of in me. (K + Mg) per liter. It can be seen from table 1, that me. (K + Mg) correspond to $10^{-4} \times$ the number of moles of PO_4 e.g. 2.5×10^{-4} moles of $\text{PO}_4 = 2.5$ me. (K + Mg).

2.3.2 Statistical analysis of experimental data

The data on yield of dry matter and on all chemical analyses are presented in the appendix. The influences of the external factors pH, K/Mg ratio, and solution concentration upon yield of dry matter and elements were examined by means of analyses

as affected by potassium-to-magnesium ratio, pH, and nutrient concentration in water-culture solution

P	Tops/ Ch-Mg	Ch-Mg/ Mg	K/Mg	Ca/Mg	K/Ca	N/Mg	P/Mg	K + Mg	K + Mg + Ca
3.77*	7.08**	< 1	12.89**	3.13*	15.36**	9.04**	11.20**	6.59**	1.38
9.44**	3.12*	115.30**	197.63**	104.56**	31.83**	182.37**	159.57**	20.32**	11.90**
68.55**	6.70**	< 1	< 1	3.83*	67.20**	< 1	1.22	39.77**	97.87**
01.88**	—	—	644.54**	716.66**	257.32**	699.20**	213.21**	204.68**	395.58**
2.64	—	—	< 1	1.60	13.15**	1.95	5.13**	1.74	9.08**
11.00**	—	—	50.84**	48.45**	6.26**	38.84**	12.81**	2.83*	5.60**
38.46**	—	—	< 1	16.17**	129.31**	1.50	4.30**	1.78	11.35**
2.03*	3.32**	5.36**	3.03**	1.99*	< 1	2.41**	1.97*	< 1	< 1
2.03	1.31	< 1	2.42*	1.47	< 1	2.00	3.28**	1.79	3.03**
1.45	< 1	< 1	< 1	< 1	1.41	< 1	< 1	3.04**	3.31**
1.75	—	—	< 1	< 1	< 1	< 1	< 1	< 1	< 1
< 1	—	—	< 1	< 1	1.58	< 1	1.41	1.78	2.50*
< 1	—	—	< 1	< 1	1.42	< 1	< 1	1.21	1.96*
< 1	—	—	< 11	< 1	< 1	1.15	1.37	2.07**	2.00**
< 1	—	—	1.1	< 1	< 1	1.05	1.07	< 1	< 1
11.74	17.19	14.87	31.20	35.56	16.98	28.26	30.98	8.29	7.44

* . . . significant at the 5% level

** . . . significant at the 1% level

of variance and of multiple regression techniques. Presentation of interaction of factors was made in the form of graphs. D values were calculated for significance at the 5% level in order to test all comparisons among means. The test employed was that of TUKEY (1953), as modified by SNEDECOR (1956).

In the analyses of variance, tests of significance were performed by computing F values (SNEDECOR, 1956). Standard deviations were expressed as a fraction of corresponding means. The resulting statistics (coefficients of variation) serve as estimates of variability among replicate determinations.

All F values are presented in table 5. The biological interpretation of the values is presented in the following. For reasons of convenience and brevity, further mention of the level of significance is omitted. Whenever of interest, such levels can be found in the table.

2.3.3 Yield of dry matter

Yield of dry matter was increased at higher pH levels. Yields of tops were more stimulated by pH increases than were root yields. Maximum stimulation was found at the lower K/Mg ratios and at the higher solution concentrations (10 and 20 me.).

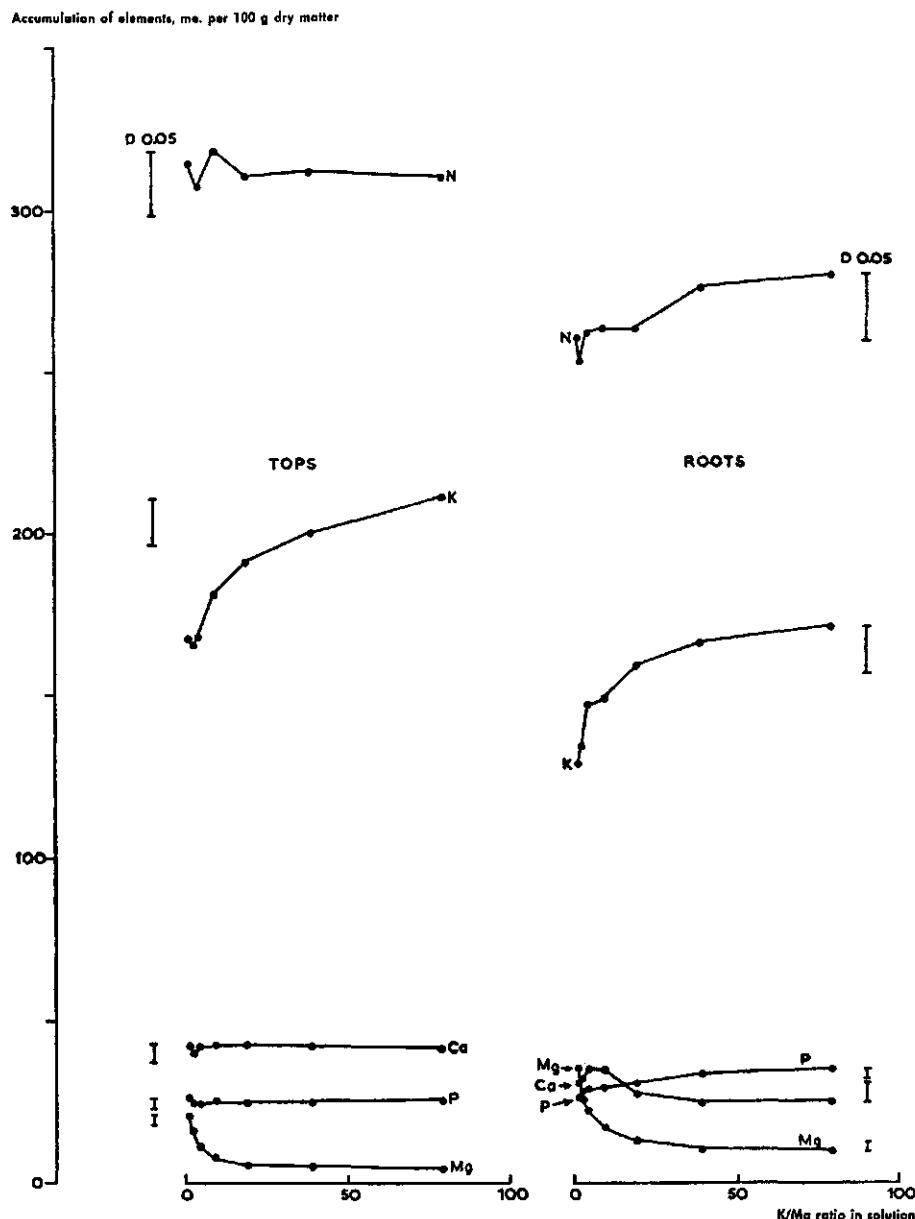


FIG. 4. Nutrient contents in tops and roots at different K/Mg ratios in solution

Yields, especially of tops, were depressed by high K/Mg ratios in the nutrient solution (fig.1). The depression was strongest at the higher solution concentrations.

Yields of tops were increased by increasing solution concentrations up to 10 me. (fig. 2). Root yields were not affected by variations in concentration in spite of apparent differences in appearance (see photographs 1 and 2, and 3 and 4).

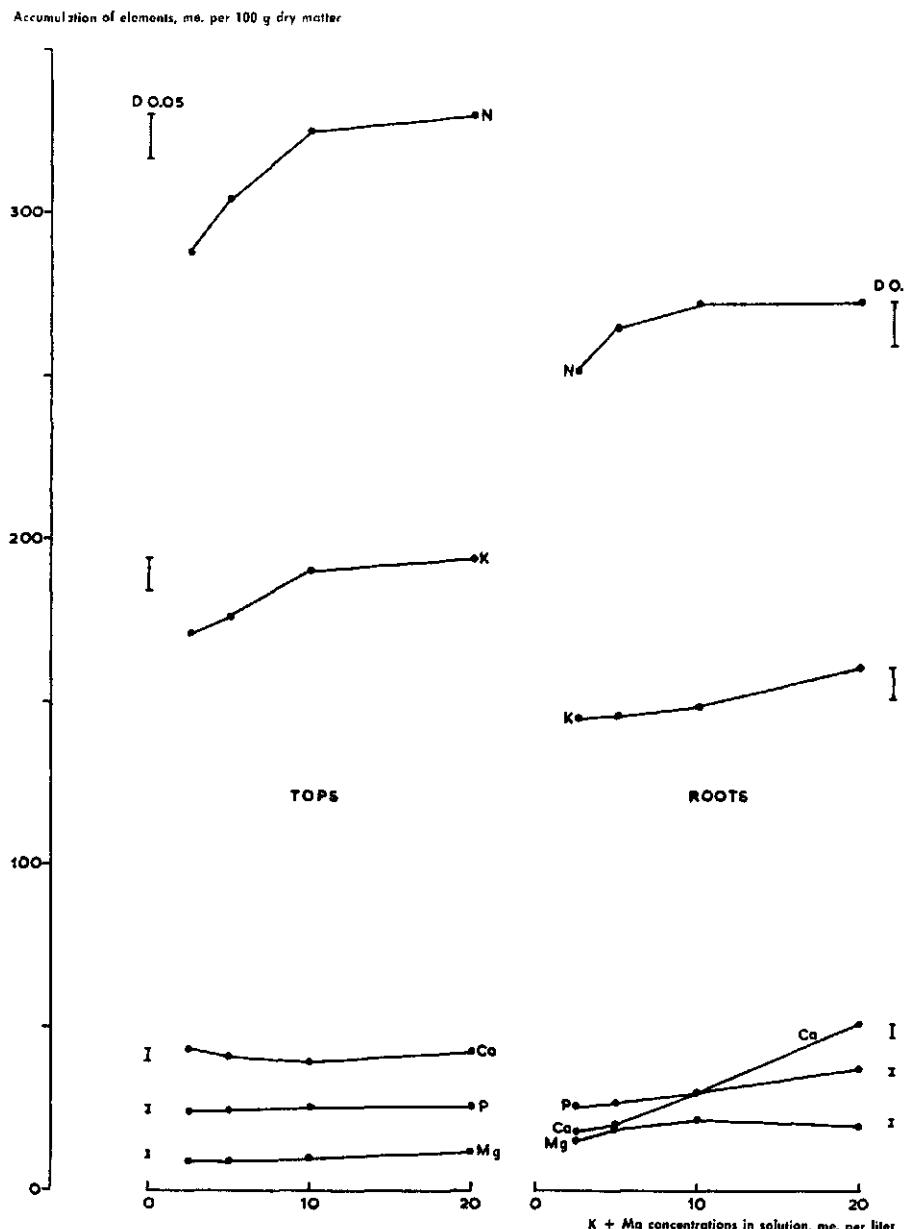


FIG. 5. Nutrient contents in tops and roots at different solution concentrations

2.3.4 K absorption

Uptake of K was higher at lower pH levels (fig. 3). As expected, K uptake increased with increasing K/Mg ratios and solution concentration (figs. 4 and 5). In tops, the rate of increase in K absorption was highest at lower solution concentrations, whereas in roots higher rates of increase were found at higher solution concentrations (fig. 5). The increase in K uptake with increasing solution concentrations was highest at pH 4 (fig. 6). Rates of increase in K uptake with increasing K/Mg ratios varied among different solution concentrations (figs. 7 and 8).

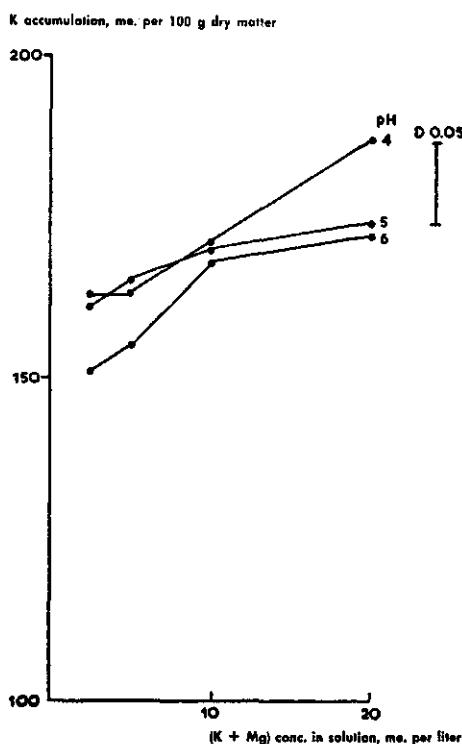


Fig. 6.

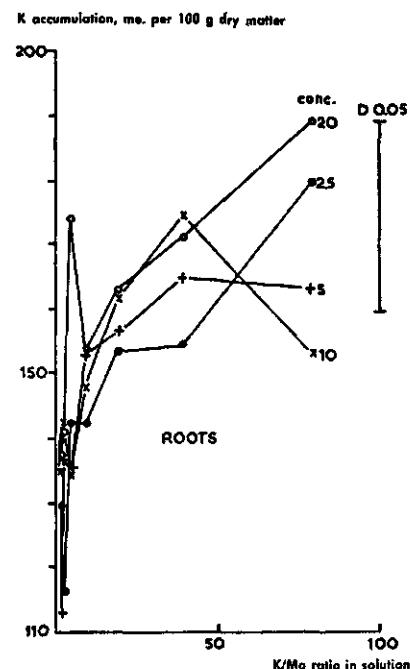


Fig. 7.

FIG. 6. Effects of nutrient concentration and pH in solution on average K accumulation in tops and roots

FIG. 7. Effects of K/Mg ratio and nutrient concentration in solution on K accumulation in tops

2.3.5 Mg absorption

Mg contents in tops were not affected by pH level, but Mg in roots increased with increasing pH (fig. 3). Mg uptake was highest at low K/Mg ratios and at high solution concentrations (figs. 4 and 5, fig. 9 and 10). For roots, the rate of increase in Mg content with increasing solution concentrations was greater than for tops. Roots

reached their maximum Mg levels at a solution concentration of 10 me., and showed a decline at 20 me. At pH 4, the decline was very marked (fig. 11).

In contrast with what was found for K, Mg contents were higher in roots than in tops (fig. 2).

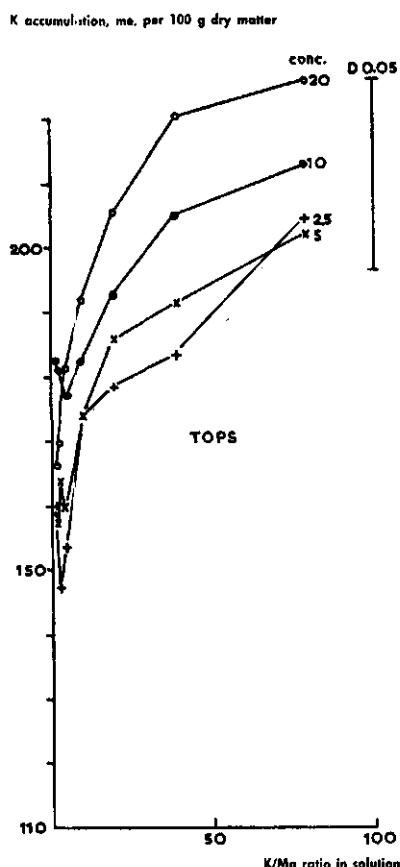


Fig. 8.

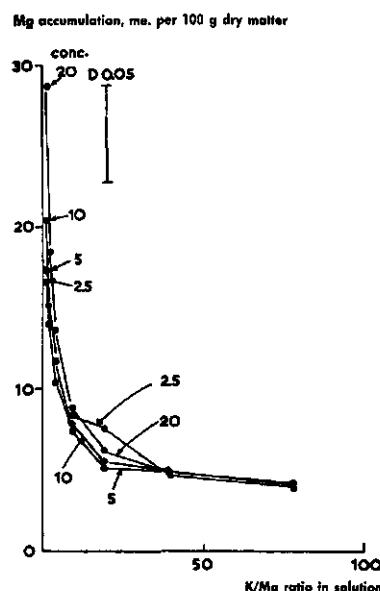


Fig. 9.

FIG. 8. Effects of K/Mg ratio and nutrient concentration in solution on K accumulation in roots
 FIG. 9. Effects of K/Mg ratio and nutrient concentration in solution on Mg accumulation in tops

2.3.6 Chlorophyll Magnesium

Chlorophyll-Mg contents were highest at the medium pH level and in the range of lower K/Mg ratios in solution. At pH 5, maximum chlorophyll-Mg levels were reached at a K/Mg ratio of 4. At other pH levels, the maxima were reached at a K/Mg ratio of 19 (fig. 12). The levels were only slightly increased by increases in solution concentration.

2.3.7 Ca absorption

No differences were found in Ca contents of tops at the three pH levels, but Ca contents in roots were higher at pH 6 than at the lower pH levels (fig. 3). These findings resemble the ones reported for Mg, for which the contents in roots were also highest at pH 6.

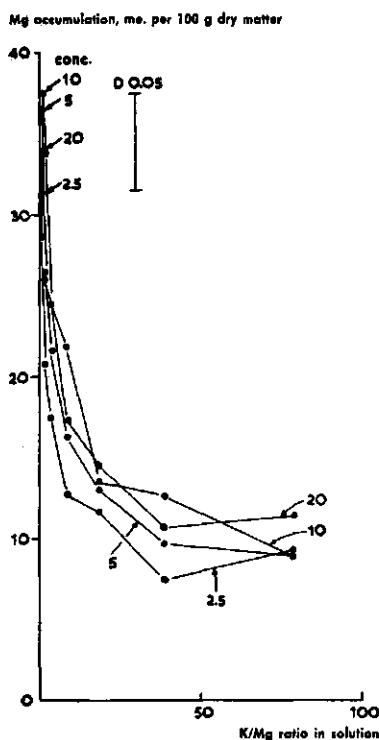


Fig. 10.

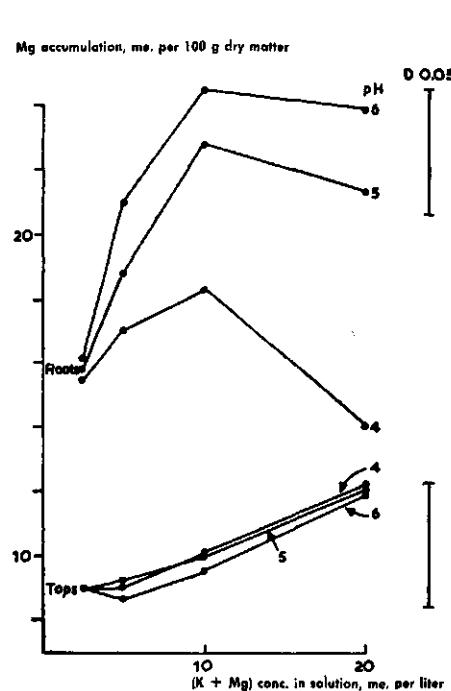


Fig. 11.

FIG. 10. Effects of K/Mg ratio and nutrient concentration in solution on Mg accumulation in roots

FIG. 11. Effects of pH and nutrient concentration in solution on Mg accumulation

Ca contents of tops were not affected by varying K/Mg ratios in solution, but in roots, maximum Ca contents were found in the range of lower K/Mg ratios especially at the highest solution concentration. The latter phenomenon was not observed for any other ion with constant concentration in solution (fig. 4).

Ca contents of roots were markedly higher at higher solution concentrations, but contents of tops remained unaffected. In roots, the rate of increase was most pronounced at higher pH levels and at low K/Mg ratios (figs. 13 and 4).

2.3.8 N absorption

Overall absorption of N was not affected by differences in pH (fig. 3), and N contents of tops remained unchanged at varying K/Mg ratios in solution. N in roots, however, increased along with K/Mg ratios (fig. 4). In tops, increasing solution concentrations

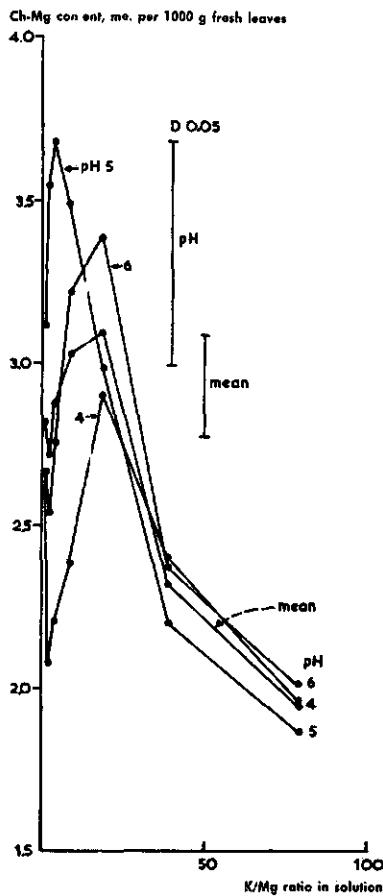


Fig. 12.

FIG. 12. Effects of K/Mg ratio and pH in solution on chlorophyll-Mg contents in leaves

FIG. 13. Effects of nutrient concentration and pH in solution on Ca accumulation

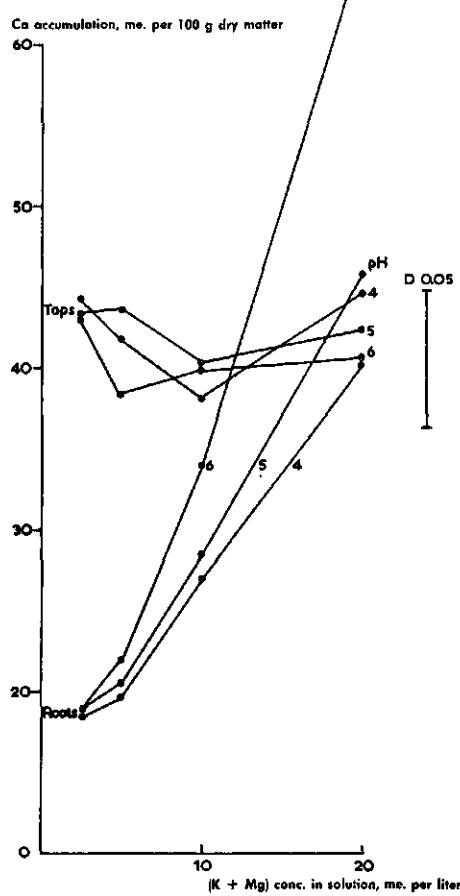


Fig. 13.

up to 10 me. resulted in higher N contents. In roots, no increases were found beyond the 5 me. level (fig. 5).

As was the case with K and Ca, higher contents of N were found in tops than in roots (fig. 2).

2.3.9 P absorption

P contents of tops were unaffected by pH changes, but P in roots was higher at pH 4 than at the higher pH levels (fig. 3). Likewise, P contents of roots increased with increasing K/Mg ratios in solution, but P in tops was not affected (fig. 4). The latter trend was also found for N.

In tops, increases in P contents with increasing solution concentrations were slight, but sharp increases were observed in roots (fig. 5). Like Mg, P contents in roots were higher than those of tops (fig. 2).

2.3.10 The ratio yield of tops to chlorophyll magnesium ($Y/Ch\text{-Mg}$)

The ratio $Y/Ch\text{-Mg}$ reached a minimum at pH 5 due to the higher Ch-Mg contents at that pH. A minimum was found also at a K/Mg ratio in solution of 19 due to the high Ch-Mg contents at that ratio. The $Y/Ch\text{-Mg}$ ratio was higher at a solution concentration of 10 me. than at lower concentrations.

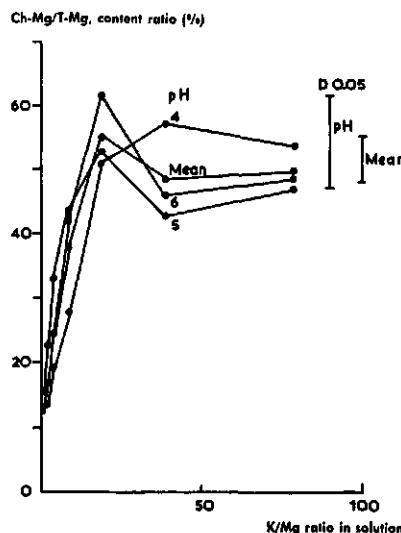


FIG. 14. Effects of pH and K/Mg ratio in solution on the ratio chlorophyll-Mg to total Mg in leaves

2.3.11 The ratio chlorophyll-magnesium to total magnesium in tops

The ratio Ch-Mg/Mg was not affected by differences in pH or solution concentration. The ratios increased sharply with increases in K/Mg values in solution up to medium levels. No further increases or slight declines in Ch-Mg/Mg values were obtained with further increases in the K/Mg ratio (fig. 14). In examining the chlorophyll-Mg contents found, it should be born in mind that these contents were determined on fresh leaf tissue and, consequently, are much higher than chlorophyll-Mg contents of total plant tops.

2.3.12 K/Mg absorption ratios

At lower pH levels, K uptake was stimulated whereas Mg uptake was depressed. Consequently, K/Mg uptake ratios were highest at pH 4. The ratio increased with increasing K/Mg values in solution (fig. 15), but the rate of increase in tops was higher than that in roots. In roots, the absorption ratios were unaffected by K/Mg ratios in solution rising from 39 to 79 (fig. 15). At the higher K/Mg ratios in solution, K/Mg absorption ratios were higher at pH 4 than at pH 6 (fig. 15).

No significant differences in absorption ratios were found at different solution concentrations. K/Mg absorption ratios in tops were higher than those in roots. In the concentration series of 2.5 and 20 me., the K/Mg absorption values were higher at

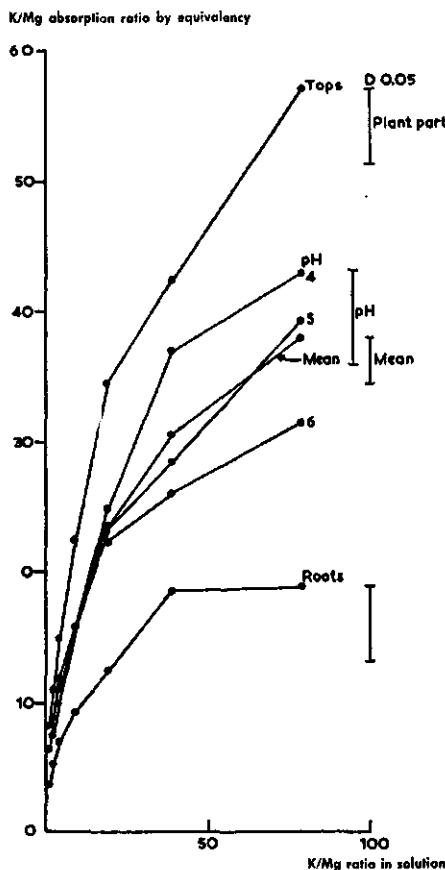


Fig. 15.

FIG. 15. Effects of K/Mg ratio and pH in solution on absorption ratio K/Mg (for pH: K/Mg values means of those for tops and roots)

Fig. 16. Effects of K/Mg ratio and pH in solution on the Ca/Mg absorption ratio (for pH:Ca/Mg values means of those for tops and roots)

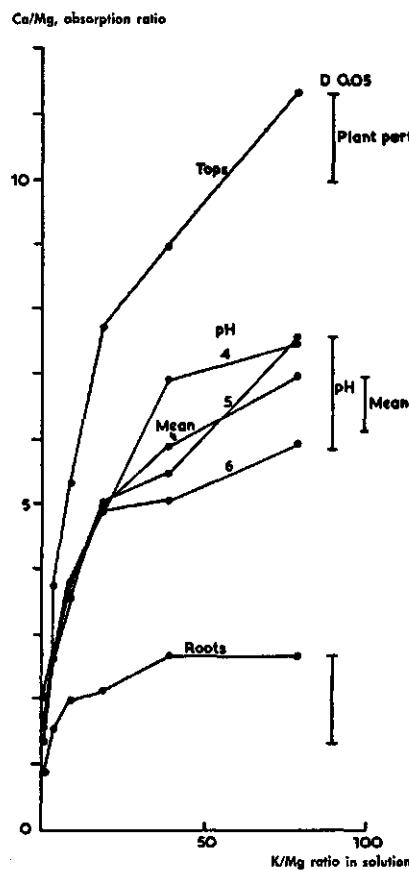


Fig. 16.

pH 4 than at pH 6. In the series of 5 and 10 me., no differences in absorption values at different pH levels were found.

2.3.13 *Ca/Mg absorption ratios*

The Ca/Mg absorption ratio was higher at pH 4 than at pH 6. With increasing pH levels, the rate of increase in Mg contents was higher than that for Ca.

With increasing K/Mg ratios in solution, Mg uptake decreased at a rate faster than that for Ca. Hence, Ca/Mg absorption ratios rose with increasing K/Mg ratios in solution (fig. 16). The rate of increase was higher in tops than in roots (fig. 16). At the lower K/Mg ratios (1 to 19), the rates of Ca/Mg increase at the three pH levels were similar. At higher K/Mg ratios (39 to 79) the increase at pH 4 was faster than at pH 6 (fig. 16).

In tops, the absorption ratio decreased with increasing solution concentrations. In roots, the trend was reversed.

In general, Ca/Mg absorption ratios were much higher in tops than in roots, due to high Ca level in tops (fig. 16).

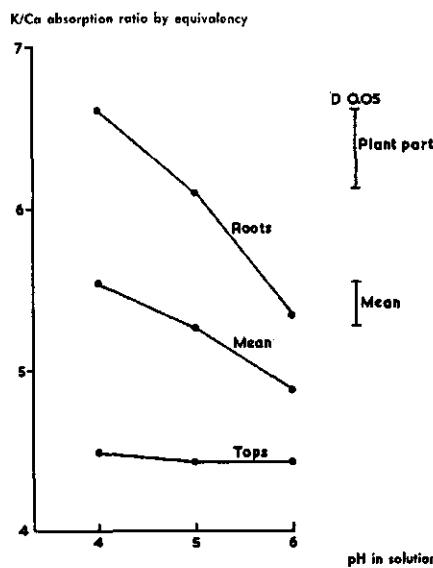


FIG. 17. Effect of pH in solution on the K/Ca absorption ratio

2.3.14 *K/Ca absorption ratios*

In tops, the K/Ca ratios showed no differences at the three pH levels. In roots, lower pH values depressed the uptake of Ca more than that of K, and, consequently, K/Ca values decreased with increasing pH levels (fig. 17).

In both roots and tops, the K/Ca absorption ratios increased with rising K/Mg ratios in solution. The rates of increase were higher for roots than for tops.

Absorption ratios in roots and tops were differently influenced by changes in solution concentration. In tops, the absorption ratios increased moderately with rising solution concentrations. For roots, the absorption ratios decreased strongly due to sharp rises in Ca contents of roots at higher solution concentrations.

In general, K/Ca absorption ratios were higher in roots than in tops (fig. 17).

2.3.15 *N/Mg absorption ratios*

In both tops and roots, the uptake ratio N/Mg was higher at pH 4 than at pH 5 and 6. In tops, the N/Mg ratio increased with increasing K/Mg ratios in solution. In roots, no significant differences were observed.

The N/Mg absorption ratio was not affected by changes in solution concentration. Similar results were obtained for the Ch-Mg/Mg ratio and the K/Mg absorption ratio. N/Mg absorption values were much higher in tops than in roots.

2.3.16 *P/Mg absorption ratios*

In tops, the P/Mg absorption ratio was not affected by varying pH levels. In roots, higher ratios were found at lower pH values.

The absorption ratios increased with increasing K/Mg ratios in solution. The rate of increase was higher for tops than for roots. At lower K/Mg ratios, the absorption ratios were similar among pH series, but at higher K/Mg values in solution, higher absorption ratios were found at lower pH values.

Differences in absorption ratios with changing solution concentrations were slight. In the 5 and 10 me. series, pH changes had no influence on the uptake ratios. In the 2.5 and 20 me. series, higher ratios were found at lower pH values. This trend was similar to that found for the absorption ratio K/Mg. Uptake ratios were higher in tops than in roots.

2.3.17 *Absorption of (K + Mg)*

Absorption of (K + Mg) was highest at pH 4, mainly due to higher K levels at that pH.

(K + Mg) absorption values at different K/Mg ratios in solution closely followed those found for K, and were higher at high K/Mg values. Furthermore, absorption values increased with solution concentration and were higher in tops than in roots.

2.3.18 *Absorption of (K + Mg + Ca)*

For roots, no differences in total cation contents were found at the three pH levels. In tops, the contents were higher at pH 4 and 5 than at pH 6.

For tops, increasing K/Mg ratios in solution stimulated cation accumulation. In roots, no differences were found.

The rate of increase in uptake values with rising solution concentrations was larger in roots than in tops.

2.3.19 Multiple Regression

Multiple-regression equations were calculated to test the relative importance of the various nutrients in determining the growth of tops and roots. In the mathematical model, the yield of dry matter per pot is expressed as a linear function of the elements absorbed and of chlorophyll magnesium:

$$\hat{Y}_{D.M.} = a + b_1 X_K + b_2 X_{Mg} + b_3 X_{Ch-Mg} + b_4 X_{Ca} + b_5 X_N + b_6 X_P$$

Tests of significance of the regression coefficients in such an equation may be made by comparing the ratio of the regression coefficient to its standard error with values of *t* for the desired probability level and appropriate number of degree of freedom¹ (SNEDECOR 1956, MATHER 1960).

The following equations were obtained:

tops:

$$\begin{aligned} \hat{Y}_{D.M.} = 2.0 - 0.028^{**}X_K - 0.070X_{Mg} + 0.768*X_{Ch-Mg} - 0.138*X_{Ca} + \\ + 0.042^{**}X_N - 0.040X_P \end{aligned}$$

roots:

$$\hat{Y}_{D.M.} = 3.1 + 0.005^{**}X_K + 0.006X_{Mg} + 0.021^{**}X_{Ca} - 0.006X_N - 0.036^{**}X_P$$

Yield of dry matter is in grams per pot, and nutrient contents are in m-moles per 100 g. of dry matter, except for chlorophyll magnesium which is expressed as m-moles per 1000 g. fresh leaves.

In tops, yield of dry matter showed significant positive correlations with chlorophyll magnesium and N, and significant negative correlation with K and Ca. In roots, yield of dry matter was positively correlated with K and Ca, and negatively correlated with P.

In another series of equations, the yield of Mg (\hat{Y}_{Mg}) is expressed as a linear function of yield of dry matter and of nutrients absorbed. The following equations were obtained:

tops:

$$\begin{aligned} \hat{Y}_{Mg} = 22.5 - 0.200X_{D.M.} - 0.095^{**}X_K - 2.928^{**}X_{Ch-Mg} + \\ + 0.072X_{Ca} + 0.048*X_N - 0.446^{**}X_P \end{aligned}$$

roots:

$$\hat{Y}_{Mg} = 0.1 + 4.257X_{D.M.} - 0.139^{**}X_K + 0.189X_{Ca} + 0.107^{**}X_N - 0.237X_P$$

In tops, yield of Mg showed a significant positive correlation with N, and negative correlation with K, chlorophyll-Mg and P. In roots, yield of Mg was positively correlated with N, and negatively correlated with K.

¹ * significant at the 5% level
** significant at the 1% level

2.4 SUMMARY OF RESULTS

A brief review will be presented of the results obtained. A more detailed evaluation of the findings will be made in combination with the results of the short-term experiments, dealt with in a later Chapter.

Mg deficiency symptoms were present in plants growing in solutions with K/Mg ratios higher than 9, regardless of pH and solution concentration. Chlorophyll magnesium contents in leaves remained high for K/Mg ratios up to 19, and the ratio chlorophyll-Mg to total Mg was constant at K/Mg ratios higher than 19. Hence, mottling symptoms in oats cannot always be expected to be a reliable index of chlorophyll-Mg contents and of chlorophyll-Mg to total Mg ratios (MAMELI 1912, RABINOWITCH 1945, HASHIMOTO 1953, 1954, 1957).

Nutrient contents were highly dependent on the composition of the nutrient solution, but in various cases also on solution concentration. In both tops and roots, K, Mg and N contents increased with increasing solution concentrations, whereas Ca and P contents increased in roots only, and remained unchanged in tops. Especially Ca contents in roots increased sharply at higher solution concentrations. This factor is of importance when considering the effect of solution concentration on the ratios of Ca to other ions in roots. Another point of interest is the possible existence of a mode of Ca uptake differing from that of other ions.

In contrast to other elements, Mg contents in roots were higher than those in tops.

The transport of Mg into tops appeared to be disturbed by high K/Mg and Ca/Mg ratios in solution (*c.f.* LUNDEGÅRDH 1932, p. 134, table 16; LUNDEGÅRDH 1951, p. 27, table 10 for oats).

The sums of cations (K + Mg) and (K + Mg + Ca) increased with rising K/Mg ratios in solution. Only the sum of the three cations in roots was found to be independent of K/Mg ratios and pH in solution.

At the lower K/Mg ratios in solution, K and Mg acted competitively in both tops and roots, as indicated by the multiple-regression equations, expressing the relationships among ions in each plant part.

In the lower range of K/Mg ratios in solution, Ca uptake, being not yet affected by high K levels, was high. With increasing K/Mg ratios, Ca uptake was depressed by high K levels.

Of the three cations examined, the uptake of Mg was most strongly depressed by low pH values in solution. K uptake, however, was higher at low pH levels. The increase was possibly associated with decreases in Mg and Ca uptake and increases in N and P uptake.

Yield of dry matter in tops showed an increase with increasing pH levels, whereas yield of roots was not affected by pH. For different pH values, K content in tops was negatively and K content in roots was positively correlated with yield. Mg contents of both tops and roots showed no correlation with yield.

As for the nutrient ratios examined, the decreases in K content with increasing pH exerted a dominant influence in lowering the K/Mg and K/Ca ratios with increasing pH. Stimulation of Mg uptake at higher pH values led to negative correlations between pH and Ca/Mg, N/Mg and P/Mg ratios.

3 SHORT-TERM WATER-CULTURE EXPERIMENTS

3.1 INTRODUCTION

Many investigations have been carried out recently to study mechanisms of ion uptake. In these studies, more or less sharp boundary lines have been drawn between passive ion uptake (also referred to as non-metabolic uptake) and active ion uptake (metabolic uptake). Each of these modes of uptake and their interrelationships are conveniently studied in short-term experiments, employing intact plants, plant tissues, or groups of cells.

LAGERWERFF (1956), and LAGERWERFF and PEECH (1961) studied whether and to what extent the initial exchange adsorption of cations (Rb and Ca) by plant roots determines their subsequent accumulation.

From the BOLTZMAN distribution law and the theory of the electric double layer, LAGERWERFF and PEECH derived a formula, that can be simplified to read:

$$a_r^+/a_r^{++} \approx 2 / (\sqrt{1 + 4(\Sigma a_r) / R^2} - 1)$$

under the assumption that roots possess a constant surface charge density. In this formula, a_r^+ and a_r^{++} are molar activities of mono- and divalent ions adsorbed on root cell membranes; a_0^+ and a_0^{++} are molar activities of mono- and divalent ions in the nutrient solution; $R = a_0^+ / a_0^{++}$; $\Sigma a_r = a_r^+ + a_r^{++}$, the total molar activity of ions adsorbed on root cell membranes.

From the experimental results on uptake of Rb and Ca by excised barley roots, they stressed that the theoretical ratio of adsorbed ions, a_r^+/a_r^{++} , calculated from the above formula did not agree with the uptake ratio as found in their experiment. Hence, exchange adsorption and accumulation of cations can be thought of as two different processes.

BROESHART (1962) also studied the relationship between cation adsorption and absorption by plant roots. Assuming a volume type of charge of roots, he used the formula

$$M_r^+ / \sqrt{M_r^{++}} = K \cdot a_0^+ / \sqrt{a_0^{++}} \dots \quad (1)$$

as derived from the DONNAN theory.

Herein, M_r^+ and M_r^{++} are the number of moles of mono- and divalent ions adsorbed by roots; a_0^+ and a_0^{++} are mono- and divalent ion activities in the ambient solution.

Assuming the root charge to be concentrated in a planar surface, the author also employed the relationship between ions adsorbed by roots and in the ambient solution as expressed in the formula

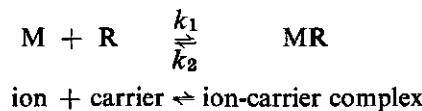
$$M_r^+/M_r^{++} = K. a_0^+/\sqrt{a_0^{++}} \dots \quad (2)$$

which was derived from ERIKSSON's formula (1952) for the double layer in clay suspensions extended from the BOLTZMAN distribution law (GAPON's equation).

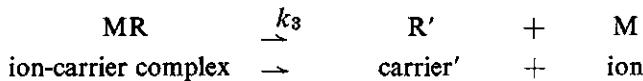
BROESHART found in an initial-uptake experiment using Na^{22} and Ca^{45} and in a sand-culture experiment with oats, that the mechanism of cation exchange in plant roots followed formula (2) assuming a constant surface charge density, and that the absorption of cations (K, Ca and Mg) is related to the ratio and not to the reduced ratio ($a_0^+/\sqrt{a_0^{++}}$) of the ions in the culture solution. From this, he inferred that adsorption and absorption are two independently occurring processes.

He also mentioned that at a constant ratio of ions in solution, the uptake ratio of ions is little affected by the salt concentration of the ambient solution and remains almost constant, and further that, when the salt concentration changes and the reduced ratios of ions ($a_0^+/\sqrt{a_0^{++}}$) are kept constant in the culture solution, the ion uptake ratio is related to the concentration of ions in the culture solution.

Employing the carrier theory, the mechanism of active ion uptake has in the past been investigated extensively for many ions (K, Na, NH_4 , Rb, Cs, Li, Ca, Sr, Ba, Cl, Br, NO_3 , SO_4 , SeO_4 , H_2PO_4 , HPO_4 , etc.). According to this theory free ions combine with carrier molecules in a reversible reaction:



The ion-carrier complex may pass through a membrane impermeable to the free ions and may subsequently be broken down metabolically in an irreversible reaction in which the bound ions are released again:



The kinetics of this reaction scheme are expressed by an analogue of the MICHAELIS-MENTEN equation for enzyme reactions:

$$i = c \cdot I / (K + c)$$

in which

i = ion uptake rate

c = ion concentration in the solution

$K = (k_2 + k_3)/k_1$ = MICHAELIS-MENTEN constant

= concentration at which $i = \frac{1}{2} I$

I = maximal rate of uptake of ion

Up till the present time, few papers have dealt with Mg uptake mechanisms. As already mentioned in chapter 1, CONWAY (1958) studied the Mg uptake mechanism in yeast

and stressed that Mg ion can be actively transported in large amounts across the yeast-cell membrane by the physiological carrier of K ions. Since this transport occurs only when Mg ions are present in appreciable concentration in the ambient solution without K, this process of Mg uptake has no physiological significance. Under such circumstances, the uptake of Mg from 0.2 molar solution is 50% inhibited by 0.5 m-mole K ions. The uptake curve descends more slowly from the 50% inhibition point than would be expected theoretically on the basis of the MICHAELIS-MENTEN kinetics, and this may be due possibly to a small residual amount of Mg absorbed by a second mechanism of Mg uptake operating between pH 3.5 and 4.5 which mechanism is not inhibited by K ions.

FRIED and NOGGLE (1958) studied mechanisms of K, Na, Rb and Sr uptake by excised barley roots and found by means of the kinetics of the carrier theory that there are two types of sites for K uptake one of which is dominant in solutions having a K concentration of more than 1 me., while the other is dominant in solutions containing less than 0.1 me. K. The MICHAELIS-MENTEN constant of the latter mechanism was found to be clearly affected by H ions in solution, although the maximal uptake (I) remained unchanged. This may mean that H ions directly compete with K ions for this site.

HANSON and KAHN (1957) studied the mechanism of K uptake by serial sections of corn root tips employing the carrier theory. In their experiment, the kinetic constants K and I changed with growth and stage of maturity, and the nature and extent of the change was conditioned by the presence or absence of Ca ion. They conclude that K is accumulated by means of a complex of carriers operating independently or sequentially, and that elements of the complex are changed during growth and maturation.

MIDDLETON *et al.* (1960) also studied the mechanisms of K and Cs uptake by excised roots and intact barley plants using K⁴² and Cs¹³⁷ in experiments lasting from 1 to 2 hours. They examined the relative rates of uptake of Cs and K by means of the observed ratio (O.R. = Cs/K in the plant/Cs/K in the solution) of which the value of unity means equal relative rates of uptake of Cs and K. It was found that in excised roots, the O.R. lay in the range of 0.15 to 0.25 in external concentrations of K up to 1.0 me. per liter. At a higher concentration (10 me. per liter) the O.R. was approximately 0.4, thus indicating a lower selectivity for K at this level. On the other hand, in the case of the intact plant, the mean O.R. for roots was 0.24, irrespective of concentration (0.1 to 10 me. K per liter) whereas in shoots the external K concentration was found to have a most marked effect on the O.R. At 10 me. K per liter, the selectivity for K in transfer to the shoot was low (mean O.R. = 0.5; K was transferred at only twice the rate of Cs), but at a concentration of 0.1 me. K per liter, K was apparently transported at 10 to 20 times the rate for Cs (mean O.R. = 0.06). These results can be interpreted to mean that K uptake in barley roots proceeds via two types of sites with different affinities for K and Cs ions, and that competition exists between K and Cs for the mechanism operating at higher K concentrations.

However, the reason for the difference in behavior between excised and attached roots remains obscure. When the proportions of added stable K and Cs in the medium were varied over a wide range, the O.R. was affected by a factor of less than two.

BANGE (1959) studied the mechanisms of K and Na uptake by intact maize plants. According to this author, there are two mechanisms for K uptake, one of which is common for both K and Na uptake and dominant at higher concentrations, and the other is specific for K uptake and dominant at lower concentrations. Only one mechanism for Na was found (the K-Na-site).

BANGE (1961) further observed with intact maize plants that the specific mechanism of K-absorption is especially involved in the supply of K for transfer to the shoot, whereas the nonspecific mechanisms of K and Na uptake seem primarily operative in the supply of non-specific osmotic ion material to the roots. He suggested, however, that non-specifically absorbed K is also liable to move into the aerial parts at a rate much higher than that of Na.

BANGE (1962) advanced the idea of "ion competition" for one species of an enzyme, i.e. the competition of M_1R_1 and $M_{11}R_{11}$ for a limited amount of an enzyme E operating after ion and carrier have combined with each other. Features in which the ion competition theory and the conventional carrier competition theory (EPSTEIN and HAGEN, 1952) differ were demonstrated by BANGE for values of maximal uptake (V_{max}) and halfvalues (H).

In terms of the ion competition theory, when the ions M_1 and M_{11} coexist in the solution, the presence of M_{11} always entails a decrease in the value of maximal uptake (V_{max1}) of the ion M_1 but not even after addition of excess M_{11} does the maximal uptake of M_1 in the presence of M_{11} fall below a certain limiting value. The half-value (H_1) of M_1 is always increased by the addition of M_{11} but, again, in the presence of excess M_{11} does the half-value of M_1 in the presence of M_{11} fail to exceed a certain limit, even in the case in which M_1 and M_{11} have separate uptake mechanisms.

Using the idea of "ion competition" as presented by BANGE, TROMP (1962) discussed the possibility that in wheat, NH_4 , K, and Na are all taken up by single, separate mechanisms. The latter investigator found that the inhibition of one ion by another is never complete and that the rate of decrease in uptake rate of the inhibited ion present at a constant concentration and the rate of increase in absorption of the inhibitor at increasing concentrations show equal relationships with the concentration of inhibiting ion.

According to the carrier theory, the rate of uptake of ion can be presented as

$$\frac{du}{dt} = \frac{I \cdot k \cdot c}{1 + k \cdot c} \quad (1)$$

in which u = uptake in me., t = time in hours, $\frac{du}{dt}$ = rate of uptake, I = maximal ion uptake rate, c = ion concentration in solution, and k = the reciprocal of the MICHAELIS-MENTEN constant.

When a plant absorbs nutrients from a solution of a certain volume (W liters) and ionic concentration (c me.), the rate of ion uptake can be presented also by the following formula expressing the change in ion concentration in the ambient solution with time

$$\frac{du}{dt} = -W \frac{dc}{dt} \quad (2)$$

in which $\frac{dc}{dt}$ = ion concentration change in solution with time.

Equating (1) and (2) yields

$$\frac{I \cdot k \cdot c}{1 + k \cdot c} = -W \frac{dc}{dt} \quad (3)$$

Integrating (3) leads to

$$-W \ln c - W \cdot k \cdot c = I \cdot k \cdot t + Q \quad (4)$$

in which Q = integration constant. When $t = 0$, $c = c_0$, then

$$Q = -W \ln c_0 - W \cdot k \cdot c_0$$

Substituting this value for Q in (4) yields

$$\frac{(c_0 - c)W}{t} = I - \frac{1}{k} \frac{(\ln c_0 - \ln c)W}{t} \quad (5)$$

When the points

$$\left[\frac{(c_0 - c)W}{t}, \quad \frac{(\ln c_0 - \ln c)W}{t} \right]$$

are plotted, the maximal uptake rate I and the constant k may be determined in a manner similar to that described by HOFSTEE (1952).

Experimental data needed to evaluate such an approach were collected in short-term experiments with nutrient solutions varying in K concentration.

The same technique was not used in studying mechanisms of Mg absorption, due to its slow uptake and to difficulties encountered in determining small quantities of Mg in solution. Therefore, whenever Mg was one of the elements involved, absorption was measured by analyzing plant material 17 hours after the plants had been placed in the experimental solutions.

During the 17-hour periods, the solutions were not renewed. Nutrient depletion during the absorption period never exceeded the level of 10% of the initial concentration. Estimates of nutrient absorption were obtained by comparing nutrient contents thus found with those of plant material not subjected to the experimental treatment.

3.2 EXPERIMENTAL METHODS

Oats, variety Marne was used for all absorption experiments. Suitable plant material was obtained by growing seedlings in sand. Six days after emergence, the young

plants were transferred to a modified HOAGLAND solution. The solution contained the following salts in concentrations as indicated:

KNO_3	0.00125 <i>N</i>
KH_2PO_4	0.00025 <i>M</i>
Mg SO_4	0.0003 <i>N</i>
$\text{Ca}(\text{NO}_3)_2$	0.0025 <i>N</i>
Fe EDTA	0.00007 <i>M</i>

The salt concentrations were half of those used in the original HOAGLAND solution, except for MgSO_4 and Fe EDTA. The former was used at 3/20 times the original concentration. Accordingly, the K/Mg ratio in solution was $15/3 = 5$ versus $30/20 = 1.5$ in the original HOAGLAND solution (HOAGLAND and BROYER, 1936).

During the pre-experimental period the plants were grown in 13-liter trays. The covers of the trays were outfitted with 30 holes in which plastic discs could be placed, each disc having 7 holes. One oat plant was lowered through each hole and kept in place by wrapping a strip of foam plastic around the lower end of the stem and inserting the strip in the hole. The plants were kept in the solution for 20 days. During this period, the nutrient solution was not renewed. The water lost by transpiration was replenished daily. Therefore, at the time of transfer to the experimental solution, the plants could be designated as low-salt plants.

In the part of the investigation concerned with K absorption mechanisms, units of 70 plants or excised roots were immersed in 2-liter volumes of nutrient solution varying in K concentration. The plants were held in place as described before. The solutions were aerated and kept at 20°C . The pH was maintained at 6 by means of small additions of KOH or HCl.

Every 30 minutes, 2- to 4-ml. aliquots of the nutrient solution were sampled and analyzed for changes in K concentration. The solutions were kept until K concentrations had reached very low levels. Volume changes caused by sampling were negligible.

Mechanisms of Mg absorption were studied by immersing oat plants in culture solutions and determining Mg contents of the plant material obtained.

Twenty days after transfer to the modified HOAGLAND solution, units of 7 intact plants were immersed in 5-liter volumes of aerated nutrient solution at pH 6 and 20°C . The cultures were kept for 17 hours under fluorescent lamps. At the end of the absorption period, the roots were rinsed with demineralized water, and separated from the tops. Both plant parts were dried at 95°C , and analyzed separately for nutrient elements. Duplicate sets were employed for each treatment, and duplicate determinations were made for each sample.

Analytical procedures used were the same as those described in Chapter 2. The results of all experiments were analyzed statistically by means of analyses of variance.

3.3 EXPERIMENTAL RESULTS

3.3.1 Mechanisms of K uptake

Experiment 1

Excised roots of 70 oat plants were immersed in 2 liters of nutrient solutions containing 0.4 me. KCl per liter, and 0.4 me. KCl plus 2 me. MgCl₂ per liter, respectively.

Values for $(c_0 - c)W/t$ and $(\ln c_0 - \ln c)W/t$ were calculated and plotted (table 6). The initial concentration, c_0 , was the concentration of K in solution 2 hours after the start of the absorption period. The assumption was made that during the first two hours the non-metabolic adsorption had come to completion. W represents the solution volume in liters for 100 g. of dry roots. Thus, I represents the maximal K uptake per hour for 100 g. of dry roots.

Although no analyses were made for very low solution concentrations, it is evident from fig. 18 that two mechanisms for K uptake exist. When Mg was added to the nutrient solution, the rate of K uptake $((c_0 - c)W/t)$ was increased.

TABLE 6. Decreases in K concentration in the solutions (A) and (B) due to absorption by excised oat roots

Sampling time (hours) ¹	Sample number	(A) Initial concentration KCl 0.4 me. per liter		(B) Initial concentration KCl 0.4 me. and MgCl ₂ 2 me. per liter	
		K concentration in solution me. ²	$(c_0 - c)W/t$ for 100 g dry roots per hour ²	K concentration in solution me. ²	$(c_0 - c)W/t$ for 100 g dry roots per hour ³
0		(c ₀) 0.243		(c ₀) 0.227	
		(c)		(c)	
0.5	1	0.218	5.58	0.194	7.37
1.0	2	0.194	5.30	0.166	6.80
1.5	3	0.171	5.19	0.140	6.40
2.0	4	0.153	4.88	0.120	5.95
2.5	5	0.136	4.65	0.090	5.65
3.0	6	0.123	4.35	0.081	5.38
3.5	7	0.102	4.38	0.066	5.10
4.0	8	0.087	4.24	0.048	4.96
4.5	9	0.072	4.13	0.033	4.76
5.0	10	0.059	4.02	0.020	4.56
5.5	11	0.046	3.91	0.010	4.36
6.0	12	0.036	3.77		
6.5	13	0.023	3.68		

¹ First sampling 2 hours after start of experiment

² Dry weight of roots used in 2-liter volume : 1.83 g

³ Dry weight : 1.80 g

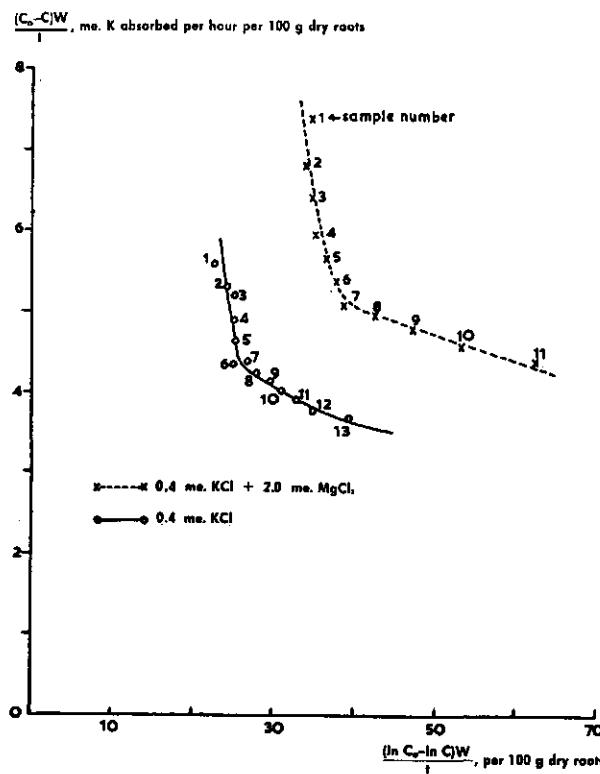


FIG. 18. Test of K absorption mechanisms, according to the carrier theory in excised oat roots

Experiment 2.

In this experiment, excised roots and attached roots of 70 oat plants were immersed each in 2 liter of solution containing 0.4 me. KCl per liter. Values for $(c_0 - c)W/t$ and $(\ln c_0 - \ln c)W/t$ are presented in table 7 and plotted in fig. 19.

In both cases, the same trend showing two mechanisms for K uptake was found. The rate of K uptake ($(c_0 - c)W/t$) was higher in attached roots than in excised roots.

3.3.2 Mechanisms of Mg uptake

Experiment 3

In this experiment, like in all other ones to follow, use is made of 5-liter volumes of nutrient solution maintained at 20°C for 17 hours. The solutions were aerated and kept at pH 6.

In the present experiment, the Mg concentration varied from 0.01 to 40 me. Mg as $MgCl_2$ per liter with and without the addition of 1 me. K per liter as KCl. Excised roots of 7 plants were used for each experimental treatment. The uptake data obtained are presented in table 8 and fig. 20. The existence of one or more Mg uptake mechanisms was tested, employing HOFSTEE's formula. The results of this test are shown in fig. 21.

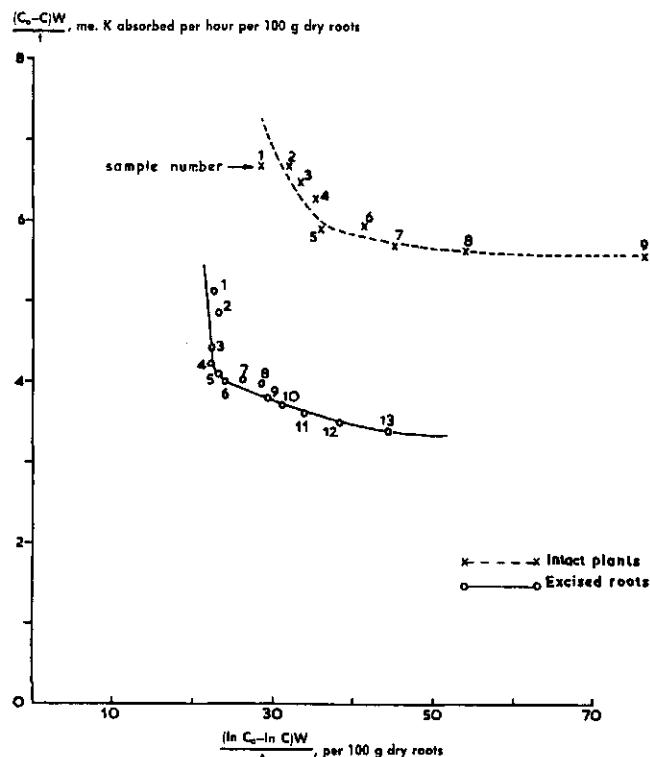


FIG. 19. Test of K absorption mechanisms, according to the carrier theory in excised roots and intact plants, using a KCl solution of 0.4 me. per liter

TABLE 7. Decreases in K concentration in solution due to K absorption by (A) excised roots, and (B) intact plants of oats

Sampling time (hours) ¹	Sample number	(A) Excised roots KCl 0.4 me. per liter		(B) Intact plants KCl 0.4 me. per liter	
		K me. in solution (c₀)	(c₀ - c)W/t for 100 g dry roots per hour ²	K me. in solution (c₀)	(c₀ - c)W/t for 100 g dry roots per hour ³
		0.232	5.12	0.240	6.67
0.5	1	0.207	4.86	0.210	6.67
1.0	2	0.184	4.43	0.179	6.67
1.5	3	0.166	4.23	0.151	6.48
2.0	4	0.148	4.10	0.121	6.26
2.5	5	0.130	4.00	0.105	5.90
3.0	6	0.113	4.02	0.077	5.93
3.5	7	0.092	3.92	0.056	5.70
4.0	8	0.074	3.79	0.033	5.62
4.5	9	0.061	3.69	0.010	5.56
5.0	10	0.049	3.59		
5.5	11	0.036	3.48		
6.0	12	0.023	3.38		
6.5	13	0.013			

¹ First sampling 2 hours after start of experiment

² Dry weight of roots used in 2-liter volume : 2.00 g

³ Dry weight of plants used in 2-liter volume : 1.84 g

TABLE 8. Exp. 3. Uptake of Mg in 17-hour period by excised oat roots from solutions with different $MgCl_2$ concentrations, containing (A) no KCl and (B) 1 me. KCl per liter

Exp. 3 (A)				Exp. 3 (B)			
$MgCl_2$ (c) me./1	Mg uptake (i) me./100 g dry matter*	$\frac{i}{c}$	K uptake me./100 g dry matter	$MgCl_2$ (c) me./1	KCl me./1	Mg uptake (i) me. 100 g dry matter*	$\frac{i}{c}$
0.00			-3.9	0.00	1		44.4
0.01	2.52	252		0.01	1	1.50	44.4
0.02				0.02	1	2.10	105
0.05	5.52	110	3.8	0.05	1	3.18	63.6
0.10	8.10	81		0.10	1	4.44	44.4
0.25	11.10	44.4		0.25	1	6.72	26.8
0.50	10.62	21.2	-3.9	0.50	1	5.94	11.8
1.00	15.96	15.9	-1.0	1.00	1	7.26	7.2
10.00	18.60	1.86	2.2	10.00	1	11.10	1.11
40.00	18.30	0.45	-3.2	40.00	1	17.90	0.45

* Initial contents in roots: Mg 3.72 me. per 100 g dry matter.
K 26.90 me. per 100 g dry matter

$$K = \frac{a_r^+ / a_{r^{++}}}{a_o^+ / a_{o^{++}}}$$

$$K = \frac{a_r^+ / a_{r^{++}}}{a_o^+ / \sqrt{a_o^{++}}}$$

$$K = \frac{a_r^+ / a_{r^{++}}}{a_o^+ / \sqrt{a_o^{++}}}$$

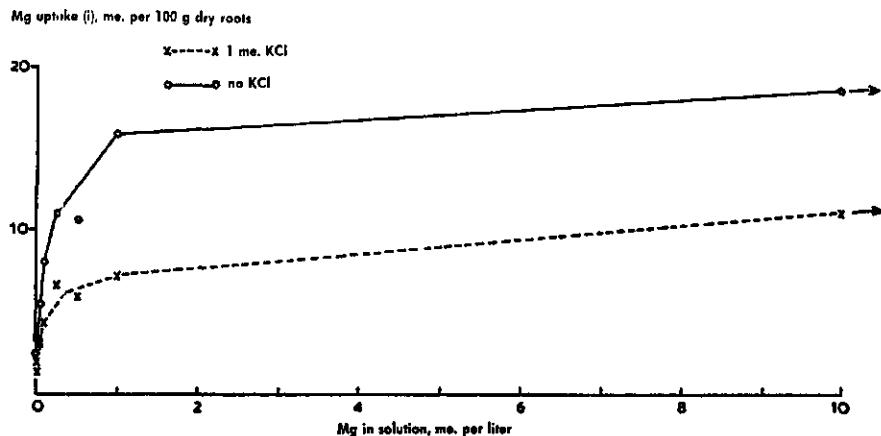


FIG. 20. Mg absorption by excised oat roots from solutions varying in $MgCl_2$ concentration, with and without KCl

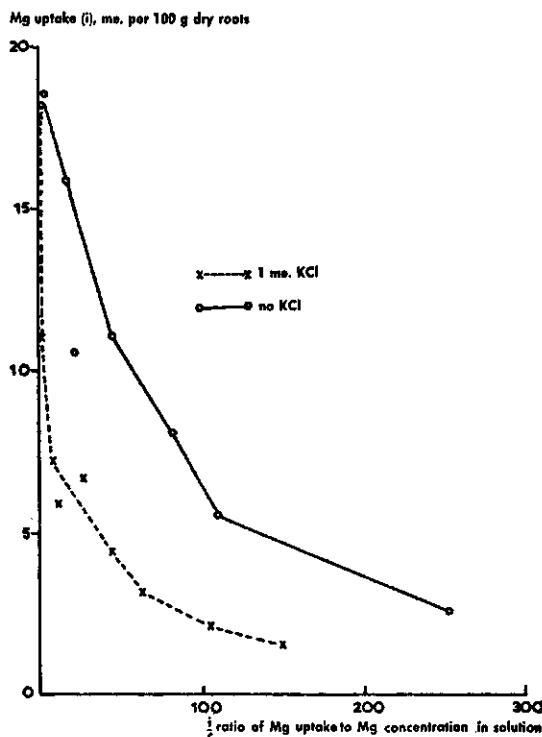


FIG. 21. Test of Mg absorption mechanisms, employing Hofstee's formula, with and without KCl in solution

3.3.3 Interaction of Mg and K in ion uptake

Experiment 4

A study was made of the uptake of both Mg and K by intact plants from solution having varying Mg concentrations (0 — 1.0 me. $MgCl_2$ per liter with and without KCl added (1 me. KCl per liter)).

The quantities of Mg and K absorbed are shown in fig. 22a and b. The initial Mg and K contents of the plants are presented in table 9. Estimates of contents and ratios of K, Mg, Ca, and P in normal oat plants can be obtained from the results of the long-term experiment, summarized in the Appendix and discussed in Chapter 2 (see also BROESHART and VAN SCHOUWENBURG (1961)).

Comparison of those data with the ones obtained in the present experiments shows that in the latter, contents of K, Mg and P were lower, and contents of Ca were higher than those found in the long-term experiment.

In the present experiment, uptake of Mg was strongly suppressed by the addition of K (fig. 22a). K uptake, however, was slightly stimulated by the presence of Mg (fig. 22b).

TABLE 9. Initial contents and ratios of elements in normal oat plants and in plants used in short-term experiments

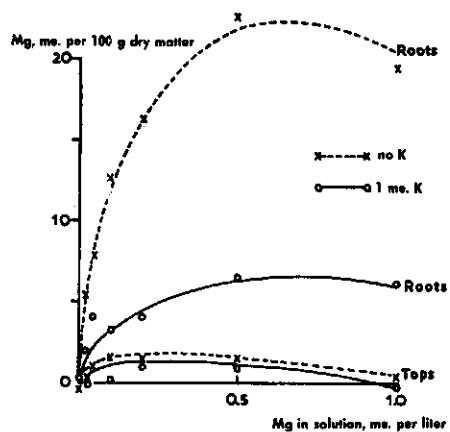
Experiment	Plant part ¹	K ²	Mg	Ca	P	K/Mg	Ca/Mg	K/Ca	P/Mg	P/K
Normal ³ plants	R	130	20	20	20	7	1	7	1	0.15
	T	150	10	40	20	15	4	4	2	0.13
4	R	11.87	15.95			0.78				
	T	27.85	7.75			3.59				
5	R	8.25	5.30			1.55				
	T	38.00	6.10			6.25				
6	R	10.14	11.43			0.88				
	T	37.70	7.30			5.16				
7	R	14.90	14.16	46.75		1.05	3.30	0.32		
	T	49.40	8.90	49.63		5.55	5.57	1.00		
8	R	11.60	17.40	44.60		0.66	2.56	0.26		
	T	51.20	8.70	51.44		5.88	5.92	1.00		
9	R	8.74	17.67		7.58	0.49			0.43	0.87
	T	36.88	7.26		4.86	5.07			0.67	0.13
10	R	11.77	15.15		7.10	0.77			0.47	0.60
	T	39.05	12.60		7.66	3.09			0.61	0.20

¹ R = Roots; T = Tops

² Data presented in me. per 100 g dry matter; P in m-moles

³ Data on normal plants taken from the long-term experiment at (K + Mg) concentrations of 2.5 and 5 me. per liter, K/Mg 4, and pH 6

(a) Mg accumulation



(b) K accumulation

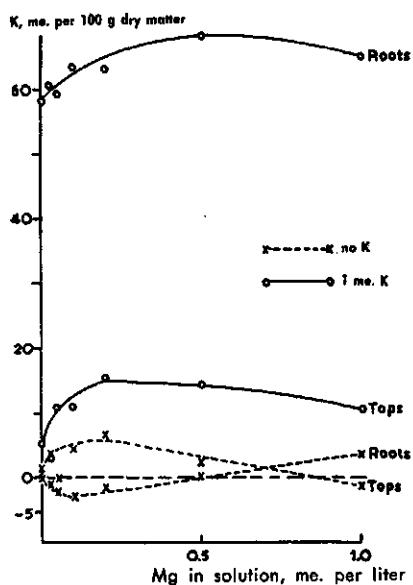
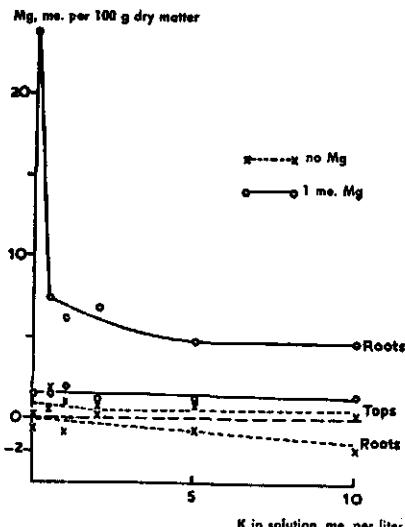


FIG. 22. Mg and K accumulation at varying Mg and constant K concentrations in chloride solutions

(a) Mg accumulation



(b) K accumulation

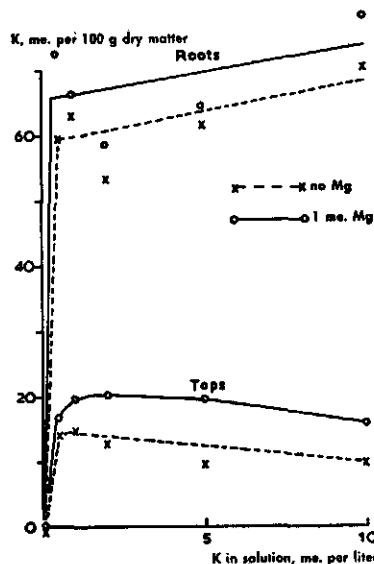
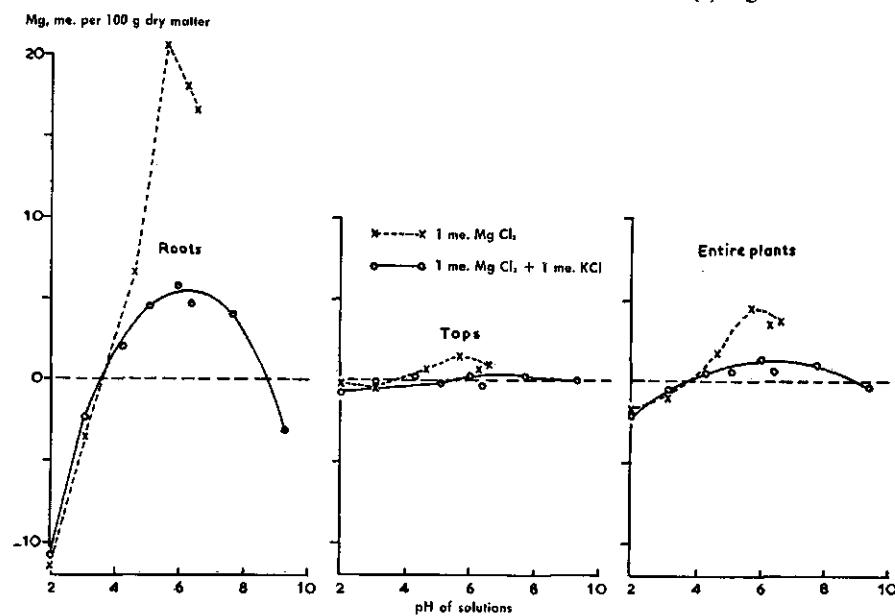


FIG. 23. Mg and K accumulation at varying K and constant Mg concentrations in chloride solutions

(a) Mg accumulation



(b) K accumulation

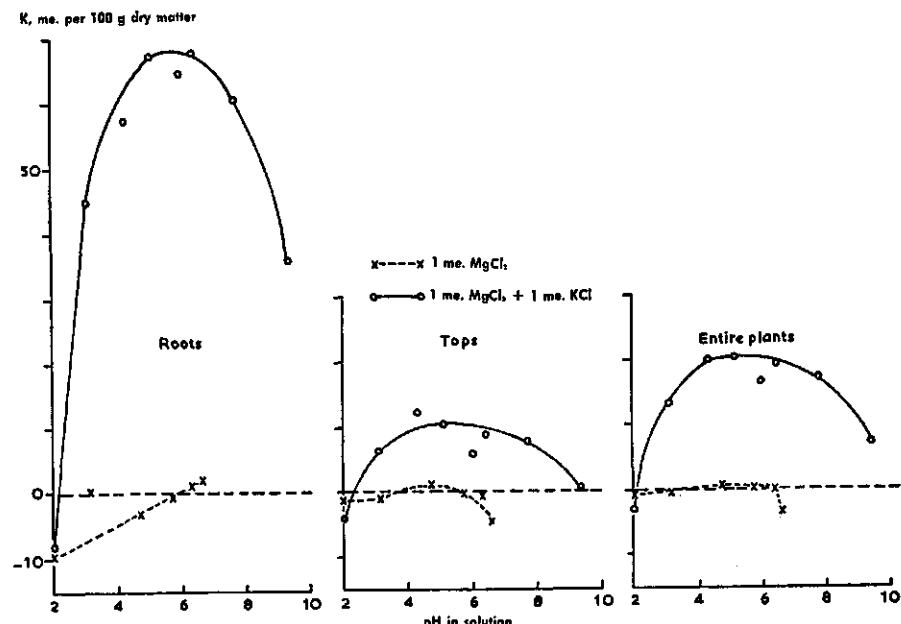
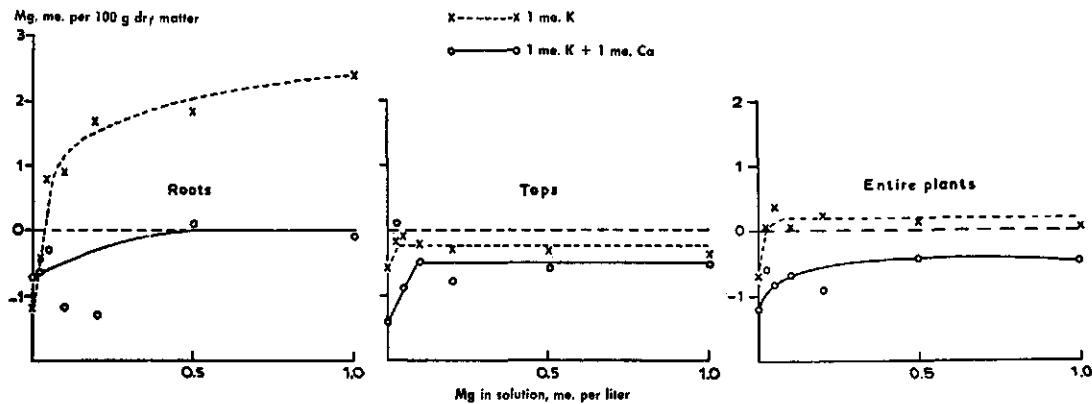


FIG. 24. Mg and K accumulation at constant Mg and K concentrations in solutions varying in pH

(a) Mg accumulation



(b) K accumulation

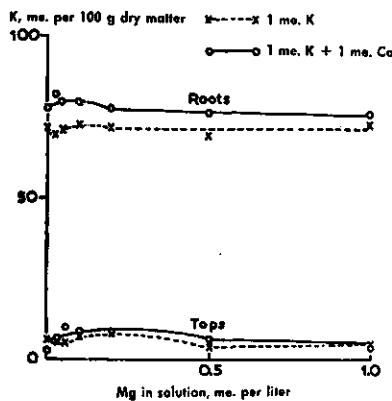
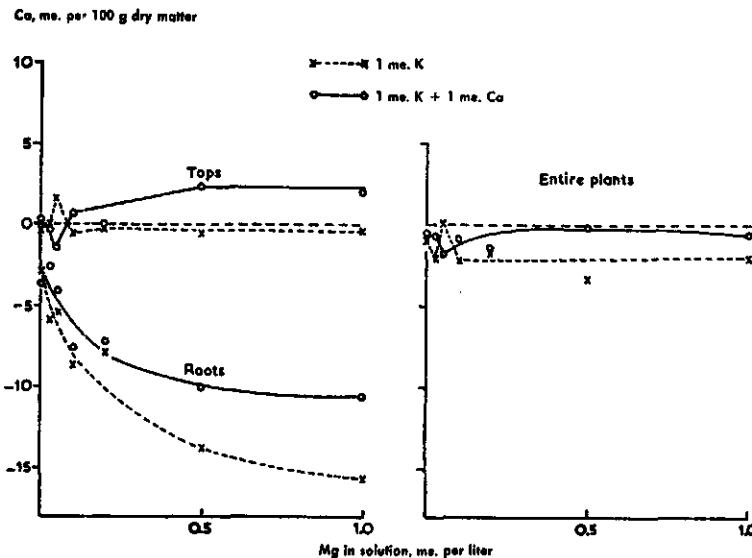


FIG. 25. K, Mg, and Ca accumulation at varying Mg and constant K concentrations in solutions, with and without Ca

(c) Ca accumulation

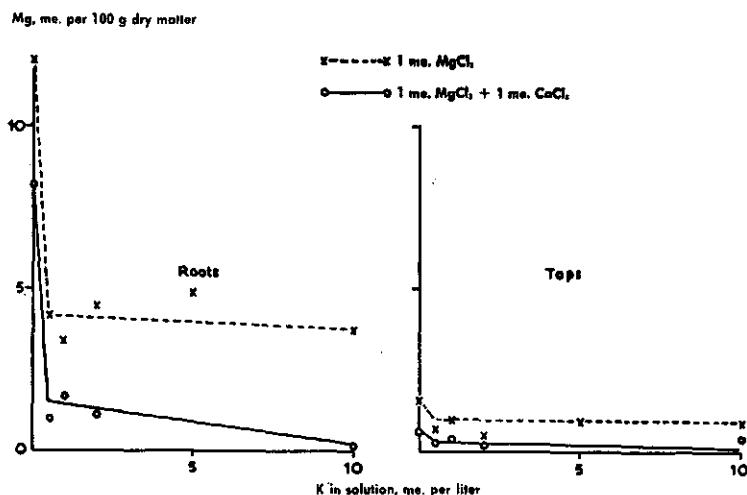


Experiment 5

In this experiment, the uptake of K and Mg by intact plants from solutions with varying K concentrations (0—10 me. KCl per liter) with and without Mg was investigated. Mg, when added, was present as 1 me. MgCl₂ per liter.

Mg accumulation in roots was strongly suppressed by the addition of K to the nutrient solution, but the rate of suppression was slight beyond the addition of

(a) Mg accumulation



(b) K accumulation

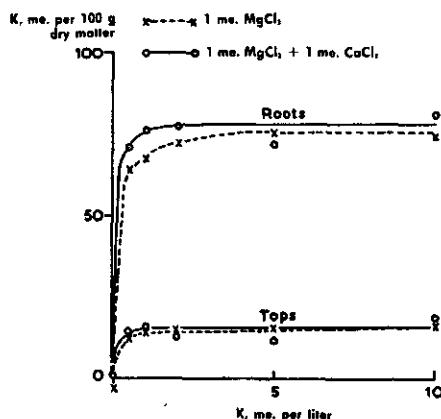


Fig. 26. K, Mg, and Ca accumulation at varying K and constant Mg concentrations in solutions, with and without Ca.

(c) Ca accumulation

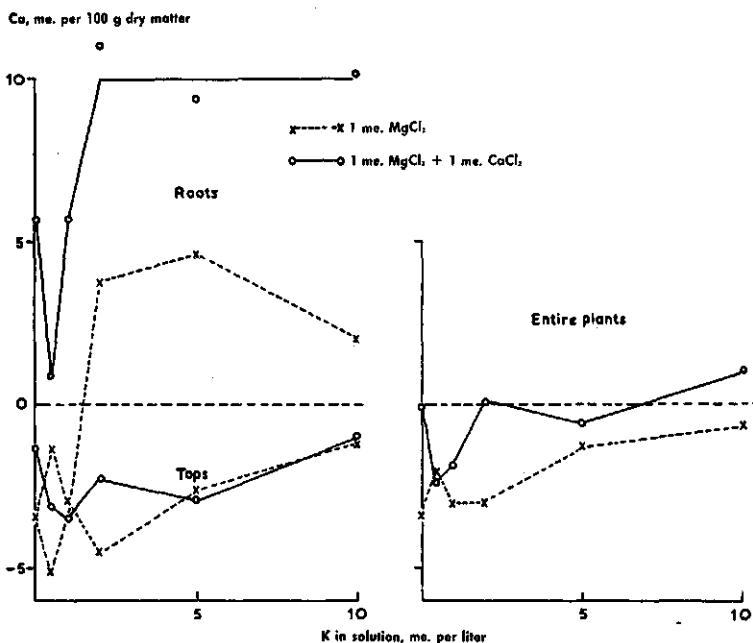


FIG. 26. (continued) K, Mg, and Ca accumulation at varying K and constant Mg concentrations in solutions, with and without Ca

0.5 me. K per liter (fig. 23 a). Little of the Mg taken up by roots during the absorption period was transported into tops (fig. 23a).

K uptake from solutions containing Mg was higher than from those containing K only (Fig. 23b).

3.3.4 Effect of pH on the absorption of Mg and K by intact oat plants

Experiment 6

Absorption of Mg and K by intact oat plants was measured at various pH values. In solutions containing 1 me. $MgCl_2$ per liter, the pH varied from 2 to 7. In other solutions containing 1 me. $MgCl_2$ and 1 me. KCl per liter, pH values ranged from 2 to 9.

Besides suppression by K, Mg uptake was strongly suppressed also by low pH (fig. 24a). Maximum absorption was found around pH 6, and Mg was lost from roots at pH values lower than 3.5.

K uptake was also depressed by low pH levels in solution (fig. 24b). Maximum absorption occurred around pH 6, but K loss from roots at low pH values was observed mainly in solutions containing no K.

3.3.5 Effect of Ca on the absorption of Mg and K by intact oat plants

Experiment 7

The concentration of Mg as $MgCl_2$ varied from 0 to 1 me. per liter. K as KCl was present at 1 me. per liter, and Ca was either present as $CaCl_2$ at 1 me. per liter, or was absent from the nutrient solution.

From fig. 25a, it can be seen that at all Mg levels in solution, Mg absorption was strongly suppressed by the addition of Ca. Comparing these results with those presented in fig. 22a, it is evident that both K and Ca inhibit the absorption of Mg, and that the combined effects of K and Ca lead to a complete cessation of Mg absorption.

K uptake was little affected by the presence of Ca and by increasing concentrations of Mg in solution (fig. 25b). Ca, although affecting the uptake of Mg, was itself not being absorbed. Fig. 25c shows that Ca was expelled into the ambient solution. The loss of Ca was even greater from those plants immersed in solutions to which Ca was not added.

Experiment 8

In this experiment Mg as $MgCl_2$ was constant at 1 me. per liter in all solutions. K as KCl varied from 0 to 10 me. per liter. Ca was either absent, or present as $CaCl_2$ at a concentration of 1 me. per liter.

Mg uptake was suppressed by the addition of K. A further suppression was brought about by adding Ca (fig. 26a). As was found before (fig. 25a), the rate of suppression of Mg by K was slight beyond the addition of 0.5 me. K per liter with and without Ca being present.

K uptake was little affected by the presence of Ca in addition to Mg (fig. 26b). In solutions containing no Ca, Ca was lost from the plants and expelled into the solution. When Ca was present in the nutrient solution, this loss of Ca was still observed at low K concentrations. At higher K concentrations, translocation of Ca from tops into roots resulted in lower Ca contents of tops and higher contents in roots (fig. 26c).

3.3.6 Effect of P on the absorption of Mg and K by intact oat plants

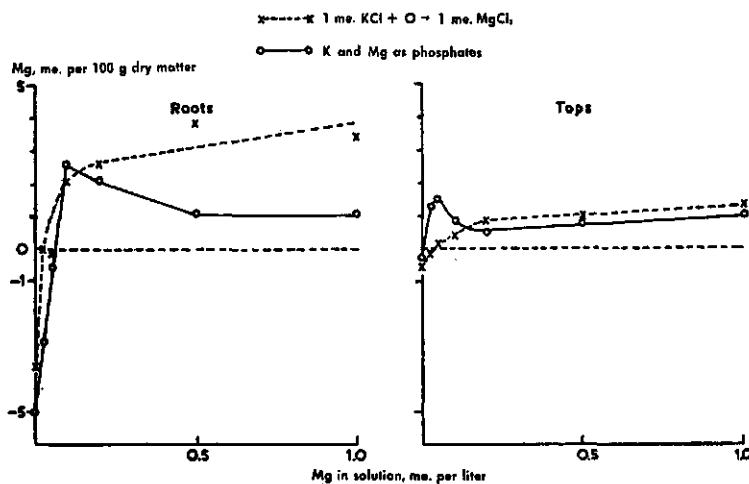
Experiment 9

The concentration of Mg varied from 0 to 1 me. Mg as $MgCl_2$. K was present in all solutions in a concentration of 1 me. as KCl . In another series, equal concentrations of K and Mg were employed, but as phosphates instead of chlorides. The concentration of $(H_2PO_4 + HPO_4)$ in the nutrient solutions varied from 1 to 2 m-moles.

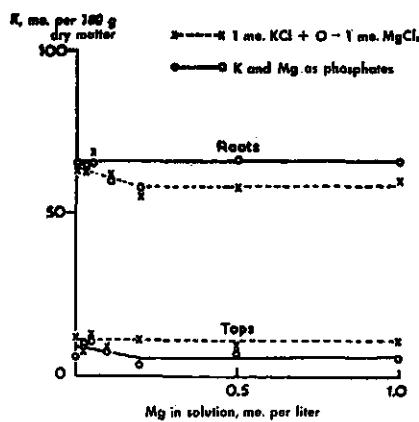
Fig. 27a shows that at higher Mg concentrations in solution, uptake of Mg was greater from chloride than from phosphate solutions. K uptake was little affected by changes in Mg concentration and by different anions (fig. 27b).

Phosphates were lost from plants growing in chloride solutions (fig. 27c). P accumulation in roots appeared to be more closely related to Mg than to PO_4 concentration in the nutrient solution.

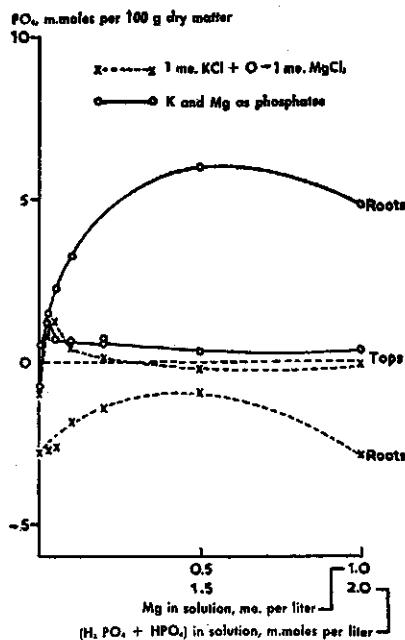
(a) Mg accumulation



(b) K accumulation



(c) PO₄ accumulation

FIG. 27. Mg, K, and PO₄ accumulation at varying Mg and constant K concentrations, present in solution as chloride or phosphates

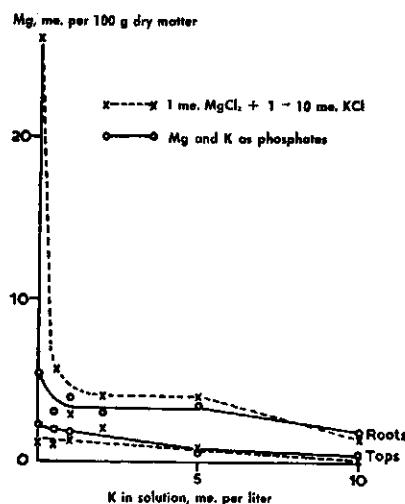
Experiment 10

In this experiment, the concentration of Mg was held constant at 1 me. per liter, and K concentration varied from 0 to 10 me. per liter. In one series, K and Mg were

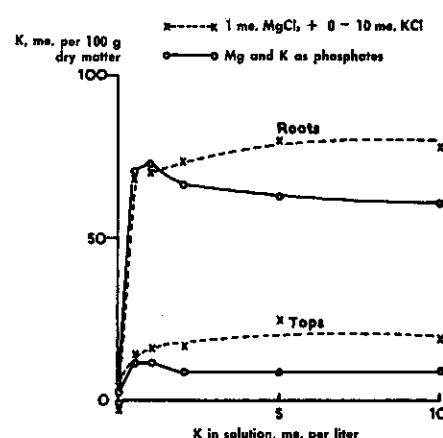
added as chlorides; in another series phosphates were used instead of chlorides. Along with variations in K, the $(H_2PO_4 + HPO_4)$ concentration varied from 1 to 11 m-moles per liter.

In the case of chlorides, Mg uptake by roots was greatly reduced by addition of 0.5 me. K per liter of nutrient solution containing $MgCl_2$. Further decreases in Mg

(a) Mg accumulation



(b) K accumulation



(c) PO_4 accumulation

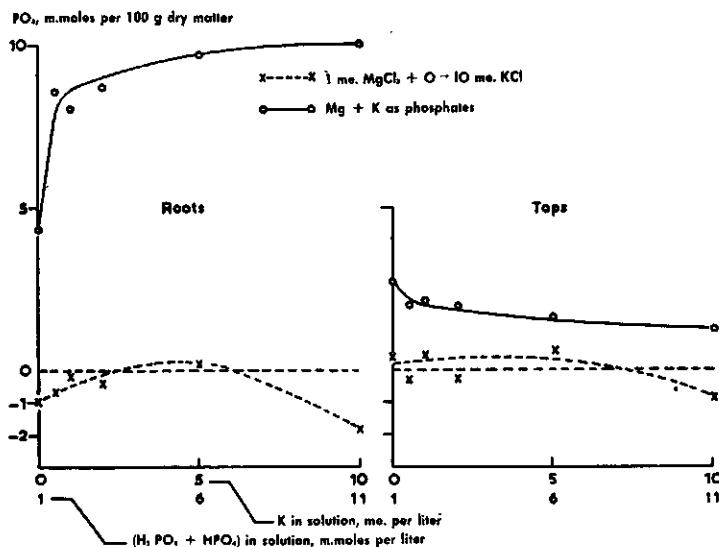


FIG. 28. K, Mg, and PO_4 accumulation at varying K and constant Mg concentrations, present in solution as chloride or phosphates

uptake at higher K concentrations were small (fig. 28a). The uptake of Mg from the solution containing Mg phosphates only was small compared to that found with Mg chlorides. Also, the reductions in Mg uptake brought about by the addition of K were slight.

In the range of higher K concentrations, K accumulation by both roots and tops was lower in the phosphates than in the chloride solutions (fig. 28b).

As was found previously, P uptake by roots seemed to be closely correlated with K uptake (fig. 28c). With the first addition of K to the solution, P accumulation in roots increased sharply, and leveled off beyond the concentration of 0.5 me. K per liter. P contents in tops were little affected by differences in concentration of K in the nutrient solution.

3.3.7 *Effect of oxygen on the absorption of Mg and K by intact oat plants*

Experiment 11

The quantities of Mg and K absorbed by oat plants from aerated and nonaerated solutions, and the K/Mg ratios in solutions and plant material are presented in table 10. The amounts of both ions absorbed from aerated solutions were higher. Especially the absorption of Mg was stimulated by aeration.

TABLE 10. Effect of aeration on accumulation of Mg and K by oat plants

Solution (me. per liter)			Treatment	Accumulation (me. per 100 g dry matter, 17-hr period)					
				roots			tops		
K	Mg	K/Mg		K	Mg	K/Mg	K	Mg	K/Mg
1	0.1	10	aeration	61.82	2.37	5.39	7.6	-0.45	5.85
			no aeration	58.53	2.01	5.29	6.5	-0.50	5.75
1	0.5	2	aeration	62.62	3.11	5.16	11.5	0.70	5.54
			no aeration	61.08	2.09	5.45	8.4	0.15	5.54
5	1	5	aeration	62.33	1.24	4.85	15.5	1.45	5.48
			no aeration	56.72	0.72	4.64	12.4	0.70	5.59
0.5	1	0.5	aeration	59.69	2.66	4.27	14.3	1.35	5.42
			no aeration	50.80	1.03	4.14	11.7	1.10	5.30
Initial contents and ratios				9.08	10.77	0.84	39.8	8.55	4.65

3.3.8 *Effect of temperature on absorption of Mg and K*

Experiment 12

The effect of different temperatures (10° and 25°C) on the uptake of Mg and K was examined in solutions varying in K concentration (0 — 10 me. KCl per liter) and with constant Mg concentration (1 me. MgCl_2 per liter). A number of the data obtained

TABLE 11. Q_{15} values of Mg uptake by intact oat plants at 10° and 25°C from solutions containing $MgCl_2$ only and ($MgCl_2 + KCl$)

Temperature (°C)	Mg uptake* from solutions containing		(1) (2)	K uptake from solution containing	
	(1) $MgCl_2$ 1 me.	(2) $MgCl_2$ 1 me. + KCl 1 me.		$MgCl_2$ 1 me.	$MgCl_2$ 1 me. + KCl 0.5 me.
	10	25		29.41	28.83
Q_{15}	3.12	4.30		3.33	1.60

* Uptake in me. per 100 g dry matter per 24 hours

are shown in table 11 and fig. 29. Q_{15} values of Mg uptake were calculated using the ratio of uptake at 25°C over uptake at 10°C. These values were calculated for the solutions containing Mg only, and Mg plus K, both at 1 me. per liter. The values obtained, 3.12 and 4.30, respectively, indicate that Mg uptake is strongly temperature-dependent.

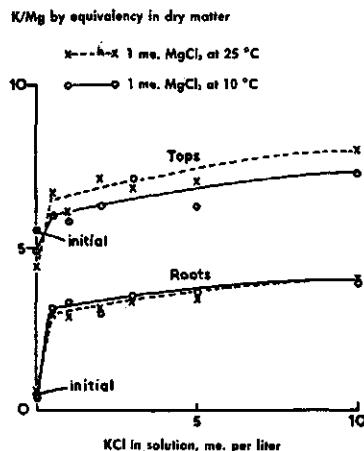


FIG. 29. K/Mg content ratio at varying K and constant Mg concentrations in solution, at 10° and 25°C

K uptake from solutions with low K concentration (0.5 me. per liter) was also found to be strongly temperature-dependent ($Q_{15} = 3.33$). At higher K concentration (1 me. per liter) the dependency of K uptake on temperature appeared to be considerably lower ($Q_{15} = 1.60$).

3.4 SUMMARY OF RESULTS

A brief discussion of the results obtained in the short-term experiments will be given here. Further evaluation of the results will be presented in the next Chapter.

Application of the carrier theory to the uptake of K in the present experiments revealed that at least two mechanisms of K uptake are operative in the roots of the oat plant, and that K uptake is stimulated by the addition of 2 me. Mg to a solution containing 0.4 me. K per liter (Exp. 1; table 6, fig. 18). The uptake of K from solutions containing 1 me. KCl per liter was not affected by additions of Mg varying from 0 to 1 me. per liter (Exp. 4, 7, and 9; fig. 22, 25, and 27), whereas K uptake was stimulated by addition of 1 me. Mg to solutions having K concentrations varying from 0 to 10 me. per liter (Exp. 5; fig. 23).

These results agree with those found by VIETS (1944), EPSTEIN (1961), and JACOBSON *et al.* (1960, 1961), who reported stimulation of K uptake by Mg. It appears that in the present experiments this stimulatory effect was more pronounced at high Mg concentrations (Exp. 5; fig. 23) than at low concentrations (Exp. 4; fig. 22), as found for Ca by EPSTEIN (1961). These findings, however, do not exclude the possibility of suppression of K uptake by Mg at concentration higher than those used in the short-term experiments (Exp. 3; table 8, fig. 20).

Again applying the carrier theory, there is evidence that two mechanisms are also operative in the uptake of Mg, one of which is dominant at higher Mg concentrations and is common for both Mg and K (Exp. 3; fig. 21). Mg uptake by this mechanism was strongly suppressed by the presence of K (Exp. 3 and 4; fig. 20a and 22a).

Mg concentrations at which the specific mechanism of Mg uptake is dominant may be less than 0.01 me. Mg per liter (Exp. 3; table 8, fig. 21).

When Mg was the single cation in solution, it was absorbed in excessive quantities taking into account the initially low content ratio K/Mg of roots and tops. The excess Mg absorbed from solutions of high Mg concentration was not transported to tops (Exp. 4 and 5; fig. 22 and 23). In this respect, Mg seems to differ from Ca, which latter element was not absorbed by excised barley roots having low K/Ca content ratios, unless K was absorbed first, as reported by HELMY *et al.* (1963).

Mg absorption took place in the pH range of 3.5 to 9. K absorption started at pH 2.5, and at pH 9, the highest level employed, uptake was still continuing. H ions competed with Mg and K for uptake in the pH range of 3.5 to 6 for Mg, and between 2.5 and 6 for K. Mg uptake was depressed by K, whereas K uptake was promoted by Mg in the pH range of 3 to 9. It can be stated that H ions compete with both Mg and K for absorption, but that K uptake is affected less than Mg uptake by H ions.

Mg absorption, already strongly suppressed by addition of K, was brought to a standstill by further adding Ca. The uptake of K was little affected by addition of Ca. Although strongly affecting the absorption of Mg, Ca itself was not absorbed during the experimental period.

In the range in which Mg uptake was strongly suppressed by K, no great differences were found in Mg absorption between chlorides and phosphates. When, however, Mg absorption was not or only partly suppressed by K levels, absorption of Mg in chloride form exceeded that of Mg phosphates.

Likewise, absorption of K added as chloride was greater than that of K associated with phosphates, although the concentration of the other cation present (Mg) was of less influence than was found for Mg absorption.

The uptake of P was closely correlated with the concentration of cations in solution. In the absence of phosphates in the nutrient solution, losses of P from plants tended to be highest at high cation concentration in solution.

Aeration and temperature increases both stimulated the uptake of cations, especially that of Mg.

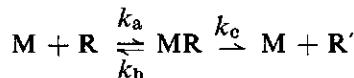
4 DISCUSSION

4.1 CARRIER THEORY

The application of the carrier theory to explain nutrient absorption phenomena observed in plants has become widespread. The theory is based on the principles of enzyme kinetics. In such an approach, the interplay of various ions in absorption processes or the lack of interplay can be explained with the aid of 4 models based on the existence of

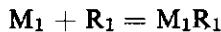
1. no inhibition
2. competitive inhibition
3. non-competitive inhibition
4. un-competitive inhibition

The general concept underlying these models is that an ion M is reversibly combined with a carrier R, and that the combination of ion and carrier moves across a membrane not penetrable for the free ion. After this transport, an irreversible reaction separates ion and carrier:



The rate of uptake (i) of an ion M is a simple function of MR and, in general, i is thought of as the rate of formation of MR.

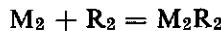
ad 1. In the model representing no inhibition, two (or more) carriers are involved in the uptake of two (or more) ions. One ion M₁ combines with carrier R₁, and the other ion M₂ combines with carrier R₂, and so on. The reactions can be written as:



for which

$$k_1 = \frac{M_1R_1}{M_1 \cdot R_1} \quad (1)$$

and



for which

$$k_2 = \frac{M_2R_2}{M_2 \cdot R_2} \quad (2)$$

The binding capacities of the carriers at saturation are denoted as I₁ and I₂, and can be written as

$$I_1 = R_1 + M_1 R_1 \quad (3)$$

and

$$I_2 = R_2 + M_2 R_2 \quad (4)$$

under the assumption that not all carrier sites available are occupied by the respective ions under consideration.

From (1), (2), (3), and (4) it follows that

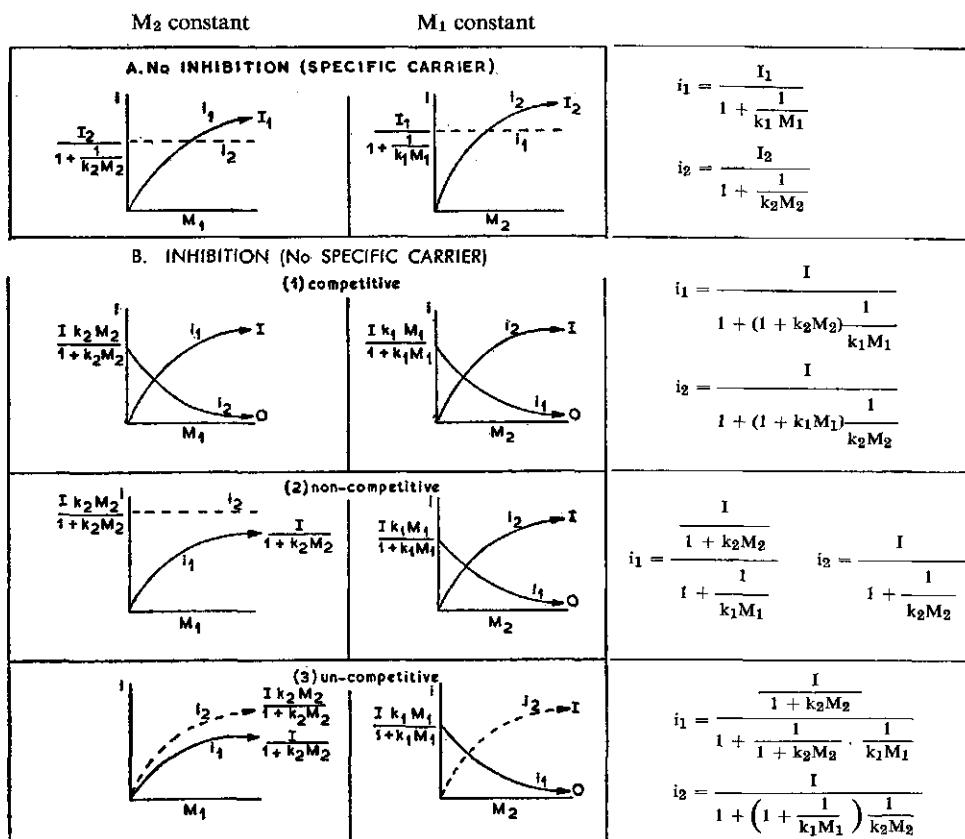
$$i_1 = M_1 R_1 = \frac{I_1 \cdot k_1 \cdot M_1}{1 + k_1 \cdot M_1} = \frac{I_1}{1 + \frac{1}{k_1 \cdot M_1}} \quad (5)$$

and

$$i_2 = M_2 R_2 = \frac{I_2 \cdot k_2 \cdot M_2}{1 + k_2 \cdot M_2} = \frac{I_2}{1 + \frac{1}{k_2 \cdot M_2}} \quad (6)$$

Rates of absorption (i) of two ions plotted versus varying concentrations (M) of one of the two ions in solution*

Mathematical formulation



* The positions of the dotted lines relative to the solid lines are arbitrarily chosen.

FIG. 30. Analysis of the carrier theory according to the mass action law

In ion absorption experiments, estimates of i_1 and i_2 can be obtained by measuring the amounts of these ions absorbed by the plants from solutions of known ionic composition. When one ion is applied at a constant concentration, and the concentration of the other ion varies, the uptake curves to be expected will have shapes as presented in fig. 30A. With increasing concentration of either one ion combined with constant concentration of the other ion in solution, the absorption values of the former approach the asymptotical values I_1 and I_2 with constant absorption values of the other ions. The positions of the horizontal lines, denoting absorption of the ions held constant, relative to the curves, are functions of the respective k values.

ad 2. In the case of competitive inhibition, two ions M_1 and M_2 compete for the binding sites on a common carrier R . Assuming different degrees of affinity for the ions and the carrier, the following equations can be presented



for which $k_1 = \frac{M_1R}{M_1 \cdot R}$ (7)



for which $k_2 = \frac{M_2R}{M_2 \cdot R}$ (8)

Furthermore,

$$I = R + M_1R + M_2R \quad (9)$$

From (7), (8), and (9) it follows that

$$i_1 = M_1R = \frac{I \cdot k_1 \cdot M_1}{1 + k_1 \cdot M_1 + k_2 \cdot M_2} = \frac{I}{1 + (1 + k_2 \cdot M_2) \frac{1}{k_1 \cdot M_1}} \quad (10)$$

and

$$i_2 = M_2R = \frac{I \cdot k_2 \cdot M_2}{1 + k_1 \cdot M_1 + k_2 \cdot M_2} = \frac{I}{1 + (1 + k_1 \cdot M_1) \frac{1}{k_2 \cdot M_2}} \quad (11)$$

In ion absorption experiments estimates of i_1 and i_2 can be obtained by measuring the amounts of the ions, absorbed by the plants from solutions of known ionic composition. When one ion is applied at a constant concentration, and the concentration of the other varies, the uptake curves to be expected will have shapes as presented in fig. 30B (I). With increasing concentration in solution the absorption of the ion varying in concentration will approach the asymptotical value I and the absorption of the other ion will approach zero.

ad 3. In the case of non-competitive inhibition, two ions M_1 and M_2 are combined with a common carrier R , but, in addition, one ion M_2 is combined with the complex formed between the carrier and the other ion M_1 . When both ions M_1 and M_2 are combined with the carrier, the one held first, M_1 is inactivated by the subsequent combination between M_1R and M_2 .



for which $k_1 = \frac{M_1R}{M_1 \cdot R}$ (12)



for which $k_2 = \frac{M_2R}{M_2 \cdot R}$ (13)



for which $k_2 = \frac{M_2(M_1R)}{M_2 \cdot M_1R}$ (14)

assuming that the affinities of M_2 for R and M_1R are the same. The binding capacity of the carrier can be presented as

$$I = R + M_1R + M_2R + M_2(M_1R) \quad (15)$$

From (12), (13), (14), and (15) it follows that

$$i_1 = M_1R = \frac{I \cdot k_1 \cdot M_1}{1 + k_1 \cdot M_1 + k_2 \cdot M_2 + k_1 \cdot M_1 \cdot k_2 \cdot M_2} = \frac{I}{1 + \frac{1}{1 + \frac{1}{k_1 \cdot M_1}}} \quad (16)$$

and

$$i_2 = M_2R + M_2(M_1R) = \frac{I \cdot k_2 \cdot M_2}{1 + k_2 \cdot M_2} = \frac{I}{1 + \frac{1}{k_2 \cdot M_2}} \quad (17)$$

From the definition of non-competitive inhibition it is evident that the degree of binding to the carrier of one of the ions involved, M_2 , is not affected by the presence or absence of the other ion M_1 . The combination of M_1 with the carrier, however, and the extent to which it is blocked by M_2 is dependent on the concentration in which M_2 is present in solution. The absorption of M_1 approaches zero when the absorption value of M_2 approaches I . Both cases are shown in fig. 30B(2). The position of the horizontal line is arbitrary and is a function of k_2 .

ad 4. In un-competitive inhibition, one ion M_1 is combined with the carrier R , while the other ion M_2 can combine only with the M_1R complex. This latter combination again leads to the inactivation of the ion M_1 originally combined.



for which $k_1 = \frac{M_1R}{M_1 \cdot R}$ (18)



for which $k_2 = \frac{M_2(M_1R)}{M_2 \cdot M_1R}$ (19)

$$I = R + M_1R + M_2(M_1R) \quad (20)$$

It follows from (18), (19), and (20) that

$$i_1 = M_1 R = \frac{I \cdot k_1 \cdot M_1}{1 + k_1 \cdot M_1 + k_1 \cdot M_1 \cdot k_2 \cdot M_2} = \frac{\frac{I}{1 + k_2 \cdot M_2}}{1 + \frac{1}{1 + k_2 \cdot M_2} \cdot \frac{1}{k_1 \cdot M_1}} \quad (21)$$

and

$$i_2 = M_2 (M_1 R) = \frac{I \cdot k_1 \cdot M_1 \cdot k_2 \cdot M_2}{1 + k_1 \cdot M_1 + k_1 \cdot M_1 \cdot k_2 \cdot M_2} = \frac{I}{1 + \left(1 + \frac{1}{k_1 \cdot M_1}\right) \frac{1}{k_2 \cdot M_2}} \quad (22)$$

The definition of un-competitive inhibition entails that combination of M_2 with carrier is preconditioned by the presence of an $M_1 R$ complex. Hence, at a constant concentration of M_2 in solution, the absorption of M_2 is dependent on a preceding combination of M_1 and R . At a constant concentration of M_1 in solution, increasing concentrations of M_2 lead to a suppression of $M_1 R$ and a preponderance of $M_2 (M_1 R)$, resulting in complete inactivation of M_1 and absorption values for M_2 approaching I (fig. 30B(3)). The positions of the dotted lines are arbitrary and depend on the numerical value of k_2 .

A study of the number and nature of carrier systems in operation is also possible when use is made of a plotting technique introduced by HOFSTEE (1952). In this approach, the amounts of an ion absorbed are plotted against the ratios of absorption value and ionic concentration in solution.

In the absence of inhibition, rewriting (5) and (6) yields the equations

$$i_1 = I_1 - \frac{1}{k_1} \cdot \frac{i_1}{M_1} \quad (23)$$

and

$$i_2 = I_2 - \frac{1}{k_2} \cdot \frac{i_2}{M_2} \quad (24)$$

On plotting values of i against values of $\frac{i}{M}$, straight lines result (Fig. 31A). The ordinate intercepts represent values for I_1 and I_2 and the slopes represent the constants

$$\frac{1}{k_1} \text{ and } \frac{1}{k_2}.$$

In the case of competitive inhibition, the equations (10) and (11) can be written as

$$i_1 = I - \frac{1 + k_2 \cdot M_2}{k_1} \cdot \frac{i_1}{M_1} \quad (25)$$

and

$$i_2 = I - \frac{1 + k_1 \cdot M_1}{k_2} \cdot \frac{i_2}{M_2} \quad (26)$$

When only one ion is present in solution, these equations attain forms identical with (23) and (24). However, in the presence of both ions in solution, the slopes of the lines are increased by factors

$$\frac{k_2 \cdot M_2}{k_1} \text{ and } \frac{k_1 \cdot M_1}{k_2},$$

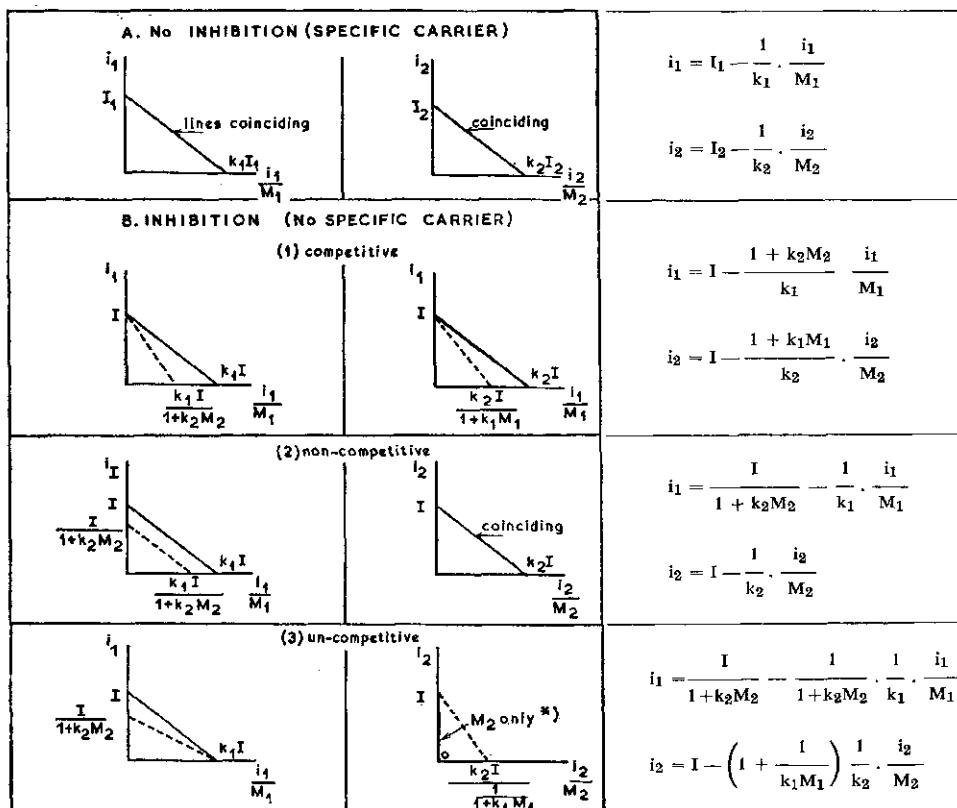
respectively. The ordinate intercepts I remain the same as found in the previous case but the abscissa intercepts are reduced to

$$\frac{k_1 \cdot I}{1 + k_2 \cdot M_2} \text{ and } \frac{k_2 \cdot I}{1 + k_1 \cdot M_1},$$

respectively (fig. 31B(I)).

Rates of absorption (i) of two ions plotted versus the ratios of i and concentration (M) of one of the two ions in solution

Solid lines: only M_1 present solid lines: only M_2 present Mathematical formulation
dotted lines: $M_1 + \text{constant } M_2$ dotted lines: $M_2 + \text{constant } M_1$



* A special case in which plants and solution contain little or no active M_1

FIG. 31. Analysis of the carrier theory employing HOFSTEE's formula

In the case of non-competitive inhibition, equations (16) and (17) can be rewritten:

$$i_1 = \frac{I}{1 + k_2 \cdot M_2} - \frac{1}{k_1} \cdot \frac{i_1}{M_1} \quad (27)$$

and

$$i_2 = I - \frac{1}{k_2} \cdot \frac{i_1}{M_2} \quad (28)$$

When only one ion is present, these equations again will be identical in form with (23) and (24). When both ions are present and when M_2 , the ion that combines with both R and M_1R , is constant, then the slope of the line resulting from plotting i_1 versus $\frac{i_1}{M_1}$ will run parallel with the line obtained for one ion. The intercepts, however, will be reduced, the ordinate one to

$$\frac{I}{1 + k_2 \cdot M_2} \text{ and the abscissa one to } \frac{k_1 \cdot I}{1 + k_2 \cdot M_2}.$$

Since in the case of non-competitive inhibition the absorption of M_2 is not affected by the presence of M_1 , the line obtained when plotting i_2 versus $\frac{i_2}{M_2}$ will coincide with the one obtained in the absence of M_1 (fig. 31B(2)).

When dealing with un-competitive inhibition, the equations (21) and (22) can be transformed to read

$$i_1 = \frac{1}{1 + k_2 \cdot M_2} - \frac{1}{1 + k_2 \cdot M_2} \cdot \frac{1}{k_1} \cdot \frac{i_1}{M_1} \quad (29)$$

and

$$i_2 = I - \left(1 + \frac{1}{k_1 \cdot M_1}\right) \frac{1}{k_2} \cdot \frac{i_2}{M_2} \quad (30)$$

In the first equation, absence of M_2 will again lead to identical forms of equations (27) and (23). In the presence of M_2 , the slope will decrease to $\frac{1}{1 + k_2 \cdot M_2} \cdot \frac{1}{k_1}$ and the ordinate intercept to $\frac{I}{1 + k_2 \cdot M_2}$. The abscissa intercept will remain unchanged (fig. 31B(3)).

Absence of M_1 will eliminate any absorption of M_2 since by definition M_2 can only combine with the M_1R carrier complex. In the presence of both M_1 and M_2 , the slope of the line obtained when plotting i_2 versus $\frac{i_2}{M_2}$ will be decreased to

$$\left(1 + \frac{1}{k_1 \cdot M_1}\right) \frac{1}{k_2}.$$

The ordinate intercept will remain unchanged, and the abscissa intercept will be reduced to

$$\frac{k_2 \cdot I}{1 + k_1 \cdot M_1}.$$

According to the enzyme kinetics involved, maximum absorption (I) never increases and upon introduction of the ion M_1 into the system, the absorption of the ion M_2 by the carrier increases only in the case of un-competitive inhibition. The condition of the constancy of I introduces the possibility of applying the present theory to biological systems in which the ion-absorption capacity must be assumed to change during the course of the experiment.

The above discussion on the various models of inhibition was based on the assumption

tion that the ions involved combine with one carrier only. In practice, however, it occurs frequently that a curvilinear relationship is found between values of i and $\frac{i}{M}$. Such a relationship may be analogous to the systems described by HOFSTEE (1952) in which two enzymes (carriers) act simultaneously and independently on the same substrate (ion). Under such circumstances, the curve obtained can be looked upon as being composed of two linear components. The difference in slope between the components can then be interpreted as a difference in affinity between the ion and the respective carriers.

4.1.1 *K absorption mechanisms according to the carrier theory*

An examination of the carrier theory requires the use of several cultural solutions differing in concentration of the ion or ions under investigation. However, when the points

$$\frac{(c_0 - c)W}{t} \text{ and } \frac{(\ln c_0 - \ln c)W}{t}$$

of equation (5) in Chapter 3 are plotted, values of I and $\frac{1}{k}$ can also be estimated with the use of only one cultural solution by analyzing the ion concentration change in solution. The latter method was employed in an investigation of the number of K absorption mechanisms and the relationship between K and Mg .

The experiments 1 and 2 reported in Chapter 3 lend themselves to an analysis of absorption mechanisms as proposed by HOFSTEE. It appears from fig. 18 that at least two mechanisms exist for absorption of K by excised roots, since both curves (A) and (B) can be resolved into two linear components. In curve (A) of fig. 18 one component defining one carrier operating at higher K concentrations, has a steep slope $(\frac{1}{k})$ and, consequently, shows a low affinity of the K ion to this carrier, suggesting a case of non-specific K absorption. At lower K concentrations, the other component indicates the presence of a carrier with a low $\frac{1}{k}$ value and a high affinity of the ion to the carrier. In this instance, the existence of a carrier specific for the absorption of K can be suggested.

In the presence of Mg (curve B), the rate of absorption of K is higher than was found for the solution containing K only. Hence, the absorption of K was stimulated by Mg . In this case, the curve can again be resolved into two linear components suggesting the presence of two carriers.

With the enzyme kinetics, a stimulatory effect can only be accounted for, when occurring in connection with un-competitive inhibition on a common carrier (table 6 and fig. 31).

It follows then that three carriers are involved in the absorption of K , one being specific for K (lower component of curve A), a second one being non-specific for K (upper components of curves A and B), and a possible third one, being common for K and Mg and showing uncompetitive inhibition of Mg by K (lower and upper components of curve B).

Strictly speaking, the concentration of Mg in solution should be kept constant

throughout the absorption period. The high initial concentration of Mg used (2 me. per liter) and the slow rate of Mg absorption by the excised roots led to depletions in Mg concentration of only 5–10% of the original concentrations. The condition of virtual constancy of the Mg concentration in solution was therefore sufficiently met.

4.1.2 *Mg absorption mechanisms according to the carrier theory*

The single-solution method used to investigate the number and nature of K absorption mechanisms was replaced by a multiple-solution method, when studying mechanisms of Mg uptake. The amounts of Mg absorbed in experiment 3 were plotted against the amounts absorbed divided by the concentration of Mg in solution (fig. 21). It can be seen from the graph that linear relationship exists between i and i/c . The positions of the curves relative to each other imply, however, that a common carrier for Mg and K exists, and that the combination of Mg and carrier is competitively inhibited by the presence of K. At lower K/Mg ratio in solution, Mg absorption increased, as shown in table 8 of experiment 3 and in the long-term experiment (figs. 7 to 10).

In experiment 4, the absorption of Mg by roots of intact plants was strongly suppressed by the addition of K (fig. 22a). Mg accumulation in tops was slight, even at higher Mg concentrations in solution, and was little affected by the presence of K in solution. Two tentative explanations can be offered for the latter findings: 1. At the start of the absorption period, the plants were high in Mg relative to K. Under such circumstances, plants exposed to cultural solutions high in Mg might be able to regulate the content ratio K/Mg in tops by limiting the movement of Mg to the tops. Any such movement might take place mainly by a specific carrier mechanism. The absorption of Mg by roots did not appear to proceed solely via a specific mechanism. 2. Transfer of Mg to tops might be a slow process requiring periods longer than 17 hours to become fully operative.

The absorption of K by roots was again slightly stimulated by increases in Mg concentration in solution (fig. 22b). Such a stimulation is compatible with the theory of un-competitive inhibition. Also in tops, small additions of Mg stimulated the accumulation of K, both in plants supplied with K and in those receiving no K in solution.

In experiment 5, Mg absorption by roots was strongly suppressed by small additions of K, but further increases in K concentration did not lead to any further depression of Mg uptake (fig. 23a). These findings can be explained by assuming that Mg absorption via a common carrier is inhibited by K, and that Mg uptake via a specific carrier is little affected by K concentrations as employed in the present experiment. The accumulation of Mg in tops was again slight during the short experimental period, but seemed little affected by K, implying that movement of Mg to tops is regulated by a specific carrier mechanism.

Fig. 23b again shows that K absorption by roots is stimulated by the presence of Mg in solution. Also the movement of K into tops appears to be stimulated by Mg.

4.1.3 *K and Mg absorption mechanisms according to the carrier theory*

In fig. 32 a schematic diagram is presented showing the possible mechanisms via which Mg and K are absorbed by oat plants in accordance with the carrier theory. At low ion concentrations in solution, the oat plant appeared to possess a specific mechanism for the absorption of both Mg and K (I_{Mg} and I_K). At higher ion concentrations in solution, two kinds of common mechanisms, competitive and un-competitive (I and I') become operative in addition to the aforementioned specific mechanisms. The competitive mechanism (I) has an affinity much higher for K than for Mg. Hence, Mg absorption from solutions relatively low in Mg by this mechanism is strongly suppressed by K. The un-competitive common carrier (I') shows a stimulation of K uptake by the presence of Mg, whereas the absorption of Mg itself via this carrier is suppressed by the presence of K in solution.

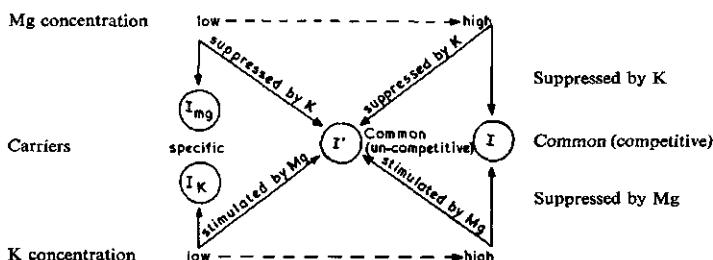


FIG. 32. Schematic diagram of the mechanisms operative in absorption of Mg and K at various concentrations in solution according to the carrier theory

4.2 ADSORPTION THEORY

Ion absorption phenomena can also be studied with the aid of physico-chemical theories based on adsorption (VAN DEN HONERT 1933, SCHUFFELEN 1946, 1954). In this approach it is assumed that the combined active sites of an adsorption surface are common for a number of cations, and that the total quantity of sites per unit weight of plant material amounts to I me. All sites are occupied by cations $C_1, C_2, C_3, \dots, C_n$ in amounts (me.) of $i_1, i_2, i_3, \dots, i_n$.

$$I = i_1 + i_2 + i_3 + \dots + i_n$$

or

$$I - i_1 = i_2 + i_3 + \dots + i_n \quad (31)$$

The cation concentrations per liter of external solutions are $M_1, M_2, M_3, \dots, M_n$.

Applying LANGMUIR's views on cation adsorption, the rate of adsorption of a cation C_1 on the adsorptive sites not yet occupied by this cation is proportional to its concentration in solution and to the number of sites occupied by other cations:

$$\text{rate of adsorption} = \frac{\Delta C_1}{t} = (i_2 + i_3 + \dots + i_n) b_1 \cdot M_1.$$

The rate of release of the cation C_1 from sites occupied by this ion is proportional to the number of sites occupied by C_1 and to the concentration of other cations in solution:

rate of release = $\frac{R_{C_1}}{t} = i_1 (b_2 \cdot M_2 + b_3 \cdot M_3 + \dots + b_n \cdot M_n)$ where b_1, b_2, b_3 , etc. are constants depending on the nature of the adsorptive surface and of the cation. When the system is in equilibrium, both rates should be equal:

$$(i_2 + i_3 + \dots + i_n) b_1 \cdot M_1 = (b_2 \cdot M_2 + b_3 \cdot M_3 + \dots + b_n \cdot M_n) i_1 \quad (32)$$

Substituting (31) into (32) yields:

$$\text{or } i_1 = \frac{(I - i_1) b_1 \cdot M_1}{b_1 \cdot M_1 + b_2 \cdot M_2 + b_3 \cdot M_3 + \dots + b_n \cdot M_n} \quad (33)$$

Equation (33) can also be written in HOFSTEE's style, as follows:

$$i_1 = I - (b_2 \cdot M_2 + b_3 \cdot M_3 + \dots + b_n \cdot M_n) \frac{1}{b_1} \cdot \frac{i_1}{M_1}$$

Equation (33) can be obtained also from the law of mass action in the case of competitive inhibition, assuming that the number of free carrier sites is negligible (see figs. 30 and 31; also BOYD *et al.* 1947, GROBLER 1959). The case, in which $b_1 \gg b_2, b_3, \dots, b_n$ corresponds with that of no inhibition in the enzyme kinetics (site specific for C_1). The adsorption theory will, however, not provide any information concerning the possible existence of non- and un-competitive inhibition systems, as considered in the conventional carrier theory based on enzyme kinetics.

The adsorption theory cannot be used to differentiate between any ion absorption phenomena other than those based upon competitive inhibition. Along this line of thinking a specific absorption mechanism can be looked upon as one showing competitive inhibition but with an infinitely low affinity of all but one of the ions toward the mechanism.

It must be stipulated in advance, that agreement of experimental data with an equation similar to (33) is not decisive in determining whether the reaction in question is one of adsorption or of chemical combination, as was pointed out by HITCHCOCK as early as 1926.

In studies on ion absorption by plants, a calculation of the ratio of quantities of 2 cations absorbed, expressed as a fraction of the ratio of concentrations of these ions in solution may be helpful in investigating absorption mechanisms (SCHUFFELEN 1950, 1954, MIDDLETON *et al.*, 1960, DE WIT *et al.*, 1963). The fraction $\frac{i_1/i_2}{M_1/M_2}$ thus obtained was called selectivity coefficient by SCHUFFELEN. A value of unity means equal relative rates of absorption of the ions C_1 and C_2 . Based on the assumption that the binding sites of the adsorptive surface are common for a number of cations,

it follows from equation (33), that the selectivity coefficient

$$\frac{i_1/i_2}{M_1/M_2} = \frac{b_1}{b_2} \quad (34)$$

Such a case is comparable to the one of competitive inhibition of two ions combined with a common carrier. Any change in ratio of concentration of the two ions C_1 and C_2 in solution would lead to equal changes in the ratio of quantities absorbed, and the selectivity coefficient would, consequently, remain constant. This applies, even when the capacities (I) of the binding mechanism per unit weight of plant material vary among different experimental treatments, provided that only one kind of binding mechanism exists.

Under conditions of no inhibition, or of non- and un-competitive inhibition, the selectivity coefficients would vary with changing ratios of ions in the external solution. Making use of the equations in fig. 30, the following relationships can be derived:

$$\begin{aligned} \text{no inhibition: } \frac{i_1/i_2}{M_1/M_2} &= \frac{I_1 \cdot k_1}{I_2 \cdot k_2} \cdot \frac{(1 + k_2 \cdot M_2)}{(1 + k_1 \cdot M_1)} \\ \text{non-competitive inhibition: } \frac{i_1/i_2}{M_1/M_2} &= \frac{k_1}{k_2} \cdot \frac{1}{(1 + k_1 \cdot M_1)} \\ \text{un-competitive inhibition: } \frac{i_1/i_2}{M_1/M_2} &= \frac{1}{k_2} \cdot \frac{1}{M_1} \end{aligned}$$

4.2.1 Use of selectivity coefficients in adsorption theory

In the case of Mg and K absorption, as studied in the long-term experiment, the resulting selectivity coefficients were plotted against concentrations of Mg in solution (fig. 33). It can be seen from the graph that values of the selectivity coefficient varied widely among the different Mg concentrations in solution. From this it can be inferred

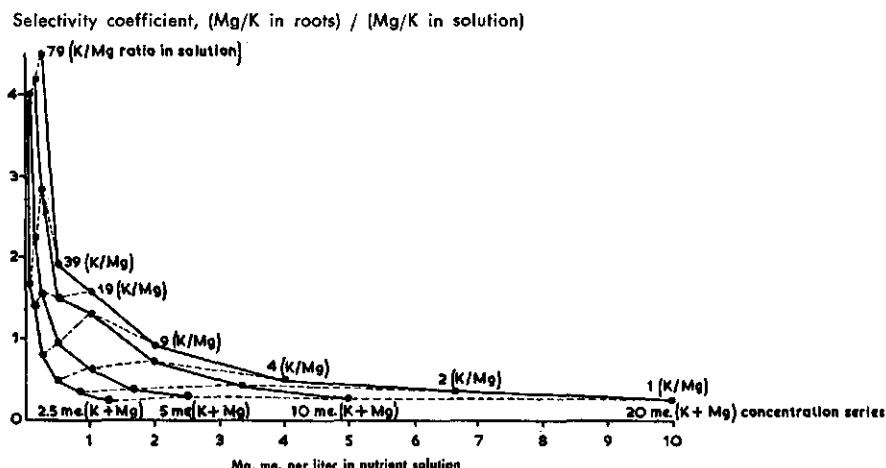


FIG. 33. Selectivity coefficient (Mg/K in roots) / (Mg/K in solution) versus Mg concentration in solution in each concentration series for roots in the long-term experiment

that absorption of Mg and K by oat plants is not regulated by means of a common binding mechanism or carrier only.

The results of the short-term experiment based on enzyme kinetics implied that at least three carriers might be operative in regulating the absorption of K and Mg. One of these can be considered to be common for both K and Mg, while the other two are specific, one for K and Mg each. At low external concentrations of any one of these ions, the specific carrier will account for practically all absorption of that ion.

Applying these results of the short-term experiments, the absorption rates of K and Mg via the common carrier in the long-term experiment can be presented with the aid of equation (33), as follows:

$$i_{k\text{-com.}} = \frac{I \cdot b_k \cdot M_k}{b_k \cdot M_k + b_{mg} \cdot M_{mg} + b_3 \cdot M_3 + \dots} \quad (35)$$

and $i_{mg\text{-com.}} = \frac{I \cdot b_{mg} \cdot M_{mg}}{b_k \cdot M_k + b_{mg} \cdot M_{mg} + b_3 \cdot M_3 + \dots} \quad (36)$

When $M_k \gg M_{mg}$, M_3 , etc. and b_k , b_{mg} , b_3 , etc. are of the same order of magnitude, $b_{mg} \cdot M_{mg} + b_3 \cdot M_3 + \dots$ will be negligibly small. Under these circumstances

$$i_{k\text{-com.}} \simeq \frac{I \cdot b_k \cdot M_k}{b_k \cdot M_k} \simeq I \quad (37)$$

Likewise, when the K/Mg ratio in solution is very low,

$$i_{mg\text{-com.}} \simeq \frac{I \cdot b_{mg} \cdot M_{mg}}{b_{mg} \cdot M_{mg}} \simeq I \quad (38)$$

K absorption by its specific mechanism can be expressed as

$$i_{k\text{-sp}} \simeq \frac{I_k \cdot b'_k \cdot M_k}{b'_k \cdot M_k + b'_{mg} \cdot M_{mg} + b'_3 \cdot M_3 + \dots} \simeq \frac{I_k \cdot b'_k \cdot M_k}{b'_k \cdot M_k} \simeq I_k \quad (39)$$

because $b'_k \gg b'_{mg}$, b'_3 , etc.

Likewise, Mg absorption by its specific mechanism becomes

$$i_{mg\text{-sp.}} = \frac{I_{mg} \cdot b''_{mg} \cdot M_{mg}}{b''_k \cdot M_k + b''_{mg} \cdot M_{mg} + b''_3 \cdot M_3 + \dots} \simeq \frac{I_{mg} \cdot b''_{mg} \cdot M_{mg}}{b''_{mg} \cdot M_{mg}} \simeq I_{mg} \quad (40)$$

because $b''_{mg} \gg b''_k$, b''_3 , etc.

At high K/Mg ratio in the solutions used in the long-term experiment, the assumptions can be made that K is absorbed by both common and specific mechanisms and that Mg is absorbed mostly via its specific mechanism. From equations (37), (39) and (40) it follows then, that

$$i_k \simeq I + I_k$$

and

$$i_{mg} \simeq I_{mg}$$

Furthermore, the selectivity coefficient will become

$$S.C. = \frac{i_m/g_{ik}}{M_{mg}/M_k} \simeq \frac{I_{mg}}{I + I_k} \cdot \frac{M_k}{M_{mg}} \simeq k \cdot \frac{M_k}{M_{mg}} \quad (41)$$

in which k is a constant.

Thus if the above assumptions are correct, the selectivity coefficient can be expected to rise with increasing concentration ratio M_k/M_{mg} in solution. Such a rise was indeed found, as can be seen from fig. 33.

When applying the adsorption theory to cases in which plants have more than one kind of binding mechanism, the assumption should be made that the average number of each kind of binding site per unit weight of plant material is approximately constant for different K/Mg ratio treatments within a concentration series. In the present investigation, concentrations of (K + Mg), H, Ca, N, and P were held constant for different K/Mg ratios within each concentration series.

It was indeed found that the sum of cation accumulation by roots was constant in each concentration series. The capacity of binding sites increased with increasing concentration of total cations in solution.

It can be stated then that, regardless of absolute Mg concentration in solution, when $\frac{M_k}{M_{mg}}$ increases, and Mg is absorbed mostly by its specific mechanism, the selectivity coefficient $\frac{i_{mg}/i_k}{M_{mg}/M_k}$ can be expected to increase.

An analysis of the data on accumulation of Mg and K in tops (figs. 7 and 9) shows that the same implications as made for roots, also hold for tops. It seems that the accumulation of Mg in tops in the long-term experiment is a reflection of the absorption of Mg by roots.

At the lowest K/Mg ratio in solution used (K/Mg = 1), the concentrations of both cations was sufficiently high to justify the assumption that they were absorbed via both common and specific mechanisms. Under such circumstances

$$i_k = i_{k-common} + I_k \quad (42)$$

and

$$i_{mg} = i_{mg-common} + I_{mg} \quad (43)$$

as can be derived from equations (35), (36), (39), and (40). In this case, the selectivity coefficient will be

$$S.C. = \frac{i_{mg}/i_k}{M_{mg}/M_k} = \frac{i_{mg-common} + I_{mg}}{i_{k-common} + I_k} \cdot \frac{M_k}{M_{mg}} \quad (44)$$

When investigating the relative values of b_{mg} and b_k for the common binding mechanism, the equations (35) and (36) account for the following relationship:

$$\frac{i_{mg-common}}{i_{k-common}} = \frac{\frac{I \cdot b_{mg} \cdot M_{mg}}{b_k \cdot M_k + b_{mg} \cdot M_{mg} + b_3 \cdot M_3 + \dots}}{\frac{I \cdot b_k \cdot M_k}{b_k \cdot M_k + b_{mg} \cdot M_{mg} + b_3 \cdot M_3 + \dots}} = \frac{b_{mg} \cdot M_{mg}}{b_k \cdot M_k}$$

Thus,

$$\frac{b_{mg}}{b_k} = \frac{i_{mg-common}}{i_{k-common}} \cdot \frac{M_k}{M_{mg}}$$

Estimates of $i_{mg-common}$ and $i_{k-common}$ can be obtained from experimental data. For

instance, from fig. 10 it can be inferred that for the lowest concentration series ($K + Mg = 2.5$ me. per liter) at a K/Mg ratio of 79:

$$i_{Mg} \simeq I_{Mg} \simeq 9.3 \text{ me. per 100 g. dry matter.}$$

In the lowest concentration series at a K/Mg ratio of 1, Mg absorption was found to be 30 me. per 100 g. dry matter (fig. 10). Using the estimate of I_{Mg} obtained above it can be stated that $i_{Mg-com} = i_{Mg} - I_{Mg} = 30 - 9.3 = 20.7$ me. per 100 g. dry matter. In the same experiment, K absorption was found to be 130 me. per 100 g. dry matter (fig. 8).

An estimate of I_K would be obtainable from a series in which the K/Mg ratio in solution would be very small. Such a series was not included in the present investigation. Only in experiment 3 (table 8), K/Mg ratios ranged from 100 to the relatively low value of 0.025. K absorption at these values was 44.4 and 21.7 me. per 100 g. of dry matter. For the purpose at hand, it is then assumed that the ratio $\frac{i_K}{I_K}$ would have a value approximately equal to that of $\frac{i_{Mg}}{I_{Mg}}$ which one was found to be $\frac{30}{9.3} \simeq 3.2$. This would lead to an estimate of I_K of $\frac{130}{3.2} \simeq 40$ me. per 100 g. dry matter, which value would lead to

$$i_{K-com} \simeq i_K - I_K \simeq 130 - 40 \simeq 90 \text{ me. per 100 g. dry matter.}$$

Thus,

$$\frac{b_{Mg}}{b_K} = \frac{i_{Mg-com}}{i_{K-com}} \cdot \frac{M_K}{M_{Mg}} \simeq \frac{20.7}{90} \times \frac{1}{1} = 0.23$$

This value, being considerably lower than unity, implies that the common binding site for Mg and K has a much higher affinity for K than for Mg.

4.2.2 Use of HOFSTEE's equation in adsorption theory

In the following discussion in which the HOFSTEE version of equation (33) was applied in order to investigate the uptake mechanisms according to the adsorption theory, three cases with different compositions of nutrient solution were considered:

1. the solution contains $Mg + H$
2. the solution contains $Mg + K + H$
3. the solution contains $Mg + K + Ca + H$.

In (1), when the concentrations of Mg and H vary, it follows from equation (33), that

$$i_{Mg} = I - \frac{b_h}{b_{Mg}} \cdot \frac{M_h \cdot i_{Mg}}{M_{Mg}}$$

Estimates of I and $\frac{b_h}{b_{Mg}}$ can be obtained by plotting the points

$$\left(i_{Mg}, \frac{M_h \cdot i_{Mg}}{M_{Mg}} \right).$$

In (2), when K and Mg concentrations vary, and the H concentration is constant,

$$i_{mg} = I - (b_k \cdot M_k + b_h \cdot M_h) \frac{1}{b_{mg}} \cdot \frac{i_{mg}}{M_{mg}}.$$

When $b_k M_k \gg b_h M_h$, this equation can be simplified to read

$$i_{mg} = I - \frac{b_k}{b_{mg}} \cdot \frac{M_k}{M_{mg}} \cdot i_{mg}.$$

Estimates of I and $\frac{b_k}{b_{mg}}$ can again be obtained by plotting the points

$$\left(i_{mg}, \frac{M_k}{M_{mg}} \cdot i_{mg} \right).$$

In (3), when Mg and K concentrations vary, and H and Ca concentrations in solution are constant,

$$i_{mg} = I - (b_k \cdot M_k + b_{ca} \cdot M_{ca} + b_h \cdot M_h) \frac{1}{b_{mg}} \cdot \frac{i_{mg}}{M_{mg}} \quad (45)$$

This equation is based on the adsorption theory assuming the existence of a common binding mechanism. In the long-term experiment, M_k changed by a factor of 2, and M_{mg} by a factor of 40. Applying the adsorption theory to this experiment, it follows from the above assumption that the term

$$\left(\frac{b_k \cdot M_k + b_{ca} \cdot M_{ca} + b_h \cdot M_h}{b_{mg}} \right)$$

in equation (45) can vary by a factor not exceeding 2. If, however, upon substitution of the experimental data in the equation the term is found to vary by a factor far different from 1 or 2, the conclusion must be drawn, that the original assumption was not valid and that, in addition to the common binding site, another type of binding mechanism must be operative.

Estimates of I and of $(b_k \cdot M_k + b_{ca} \cdot M_{ca} + b_h \cdot M_h)/b_{mg}$ can be obtained by plotting the points

$$\left(i_{mg}, \frac{i_{mg}}{M_{mg}} \right),$$

using the analytical data of the long-term experiment reported in figs. 9 and 10. The resulting curves for the 2.5 me. and 20 me. (K + Mg) series are shown in figs. 34 (a and b).

It is evident that the slopes of these curves change by factors far exceeding the value of 2, and from this the conclusion can be drawn that Mg absorption by oat plants is regulated by more than one mechanism which is common for Mg and other cations.

At high K/Mg ratios in solution, the slopes of the curves approach zero as can be seen from fig. 34. This can only be the result of infinitely small values of b_k , b_{ca} , and b_h relative to b_{mg} in the term

$$\frac{b_k \cdot M_k + b_{ca} \cdot M_{ca} + b_h \cdot M_h}{b_{mg}}$$

In other words, evidence is obtained that at high K/Mg ratios in solution the affinity of cations other than Mg for the binding mechanism has become infinitely small, and that the mechanism is specific for the absorption of Mg.

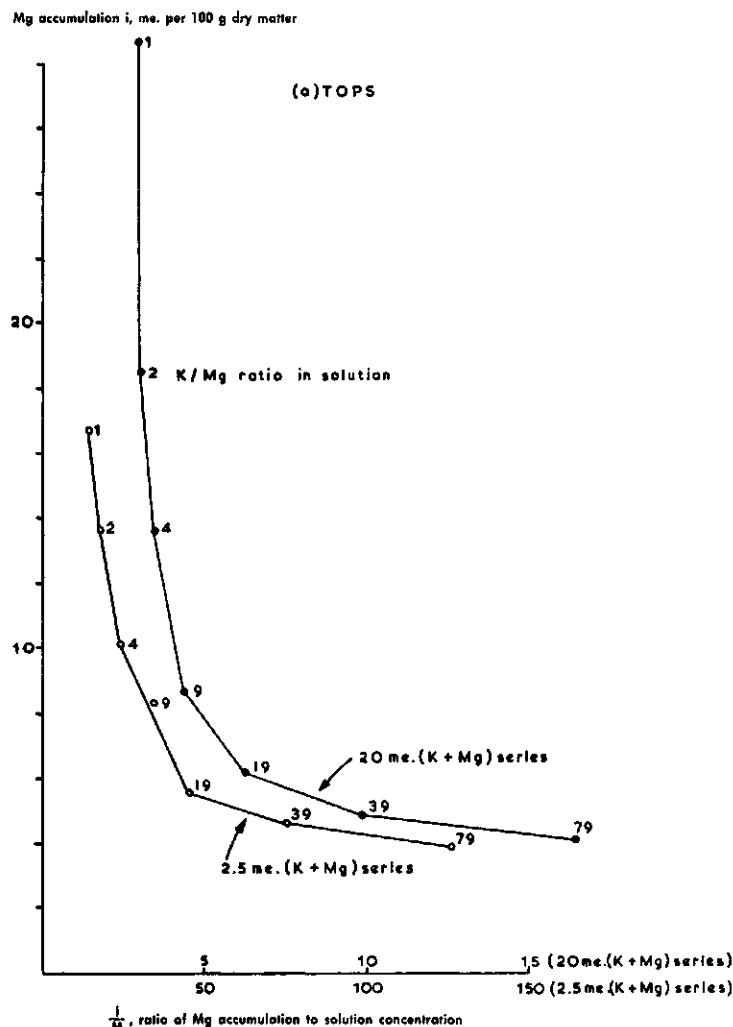


FIG. 34a. Test of Mg absorption mechanism in the long-term experiment by means of the absorption theory. Data taken from fig. 9 (tops)

The finding of a slope increasing with decreasing K/Mg ratios in solution must be attributed to increases in the values of b_k , b_{ca} , and b_h relative to b_{mg} . In other words, at decreasing K/Mg ratios, a mechanism comes into play which shows an affinity not only for Mg, but also for other cations.

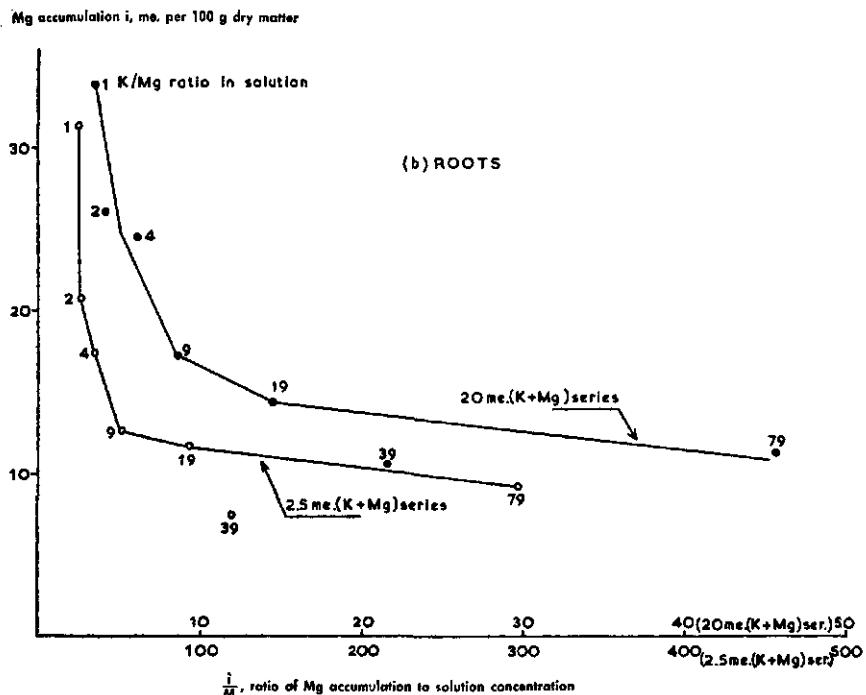


FIG. 34b. Test of Mg absorption mechanism in the long-term experiment by means of the adsorption theory. Data taken from Fig. 10 (roots)

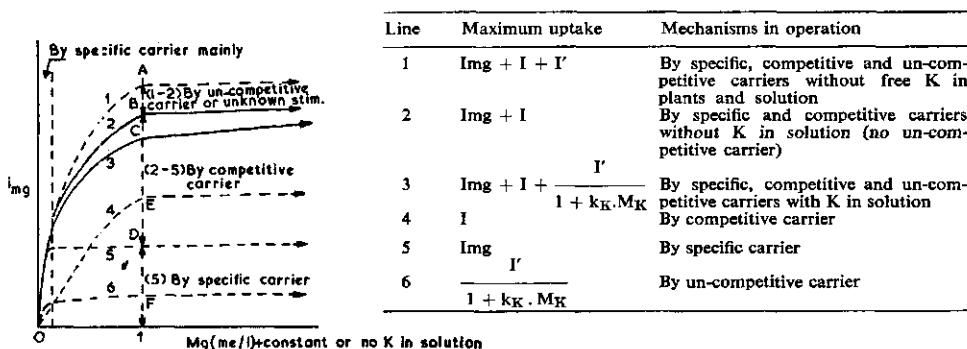
4.2.3 *K and Mg absorption mechanisms according to the carrier and adsorption theories*

The findings presented in the foregoing on the absorption of Mg and K according to the carrier and adsorption theories are graphically presented in fig. 35 and 36. Fig. 35a deals with the absorption of Mg at increasing Mg levels in solution combined with a constant K level or no K in solution. When the ambient solution contains only Mg, Mg uptake with increasing Mg concentration will proceed as pictured in curve 2. In the range of low Mg concentrations, Mg is absorbed mainly by means of its specific mechanism. At higher Mg concentrations, it is absorbed via both the mechanism specific for Mg and the competitive mechanism common for Mg and K. The distance between the curves 2 and 5 represents the uptake by the common mechanism, and curve 5 depicts Mg uptake by its specific mechanism only.

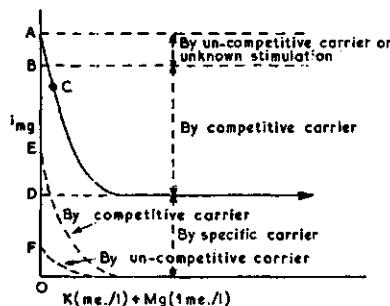
In the presence of a carrier showing un-competitive inhibition of Mg by K, besides a specific and a competitive carrier, Mg uptake follows curve 1, assuming the absence of free K in solution and plant. The distance between the curves 1 and 2 represents Mg uptake by the un-competitive carrier. When the solution contains a constant quantity of K, Mg uptake is represented by curve 3. The distance between curves 1 and 3 shows the suppression of the uptake of Mg by K at both common carriers.

competitive and un-competitive. Curve 4 depicts Mg uptake by the competitive mechanism only and curve 6 by the un-competitive mechanism only.

In fig. 35b, at an arbitrary Mg concentration of 1 me., the absorption of Mg is shown as affected by the presence of increasing quantities of K in solution. Mg uptake being at level A (as found in fig. 35a) in the absence of K (Mg uptake by specific, competitive and un-competitive carriers) will decrease to the level D (Mg uptake by its specific mechanism mainly).



(a) Mg uptake with increasing Mg and constant K concentration in solution



(b) Mg uptake with increasing K and constant Mg (1 me. per liter) concentrations in solution

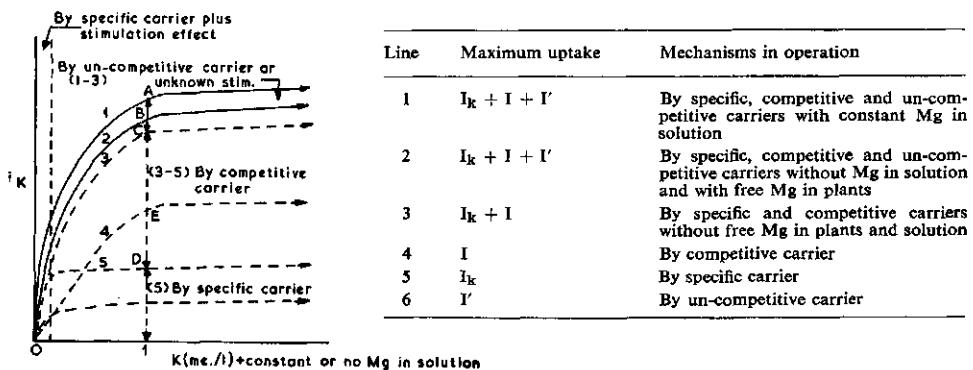
Note: Factual situations are depicted by solid lines, imaginary situations by dotted lines.

FIG. 35. Analysis of Mg uptake

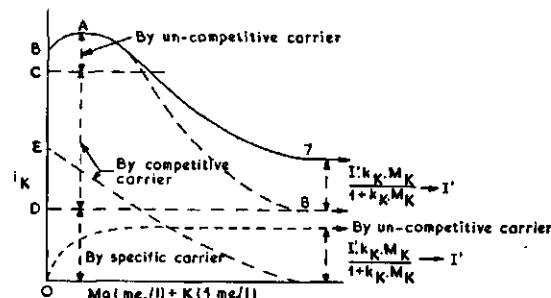
Fig. 36a shows the absorption of K from solutions with increasing K concentrations combined with a constant Mg level or no Mg in solution. When the solution contains K only, the uptake of K will follow curve 3 with increasing K concentrations in solution. In the range of low K concentrations in solution, K is absorbed mainly by its specific mechanism. At higher K concentrations, it is absorbed via both the mechanism specific for K and the competitive mechanism common for K and Mg. The distance between the curves 3 and 5 represents the uptake by the common mechanism, and curve 5 depicts the uptake by the specific mechanism.

In the presence of a carrier on which Mg uptake can be un-competitively inhibited by K, the uptake of the latter follows curve 2 assuming the presence of free or active Mg in the plant. The distance between the curves 2 and 3 represents K uptake by the stimulation effect.

When in addition to free Mg present in the plant the outer solution contains Mg in moderate quantities, K uptake will be further increased to curve 1 due to the stimulation effect by the un-competitive or by an unknown mechanism. Curve 4



(a) K uptake with increasing K and constant Mg concentration in solution



(b) K uptake with increasing Mg and constant K (1 me. per liter) concentration in solution

Note: Factual situations are depicted by solid lines, imaginary situations by dotted lines.

FIG. 36. Analysis of K uptake

depicts K uptake by the competitive mechanism only, and curve 6 by the un-competitive mechanism only.

In fig. 36b, the change in K uptake starting from level B, as found in fig. 36a (1 me. K per liter), is shown with Mg concentrations increasing from zero to very high levels. K uptake will first increase via point A (as found in fig. 36a), due to the effect of un-competitive carrier or the unknown stimulation effect. With Mg increasing in solution to levels where it starts to compete with K for sites on the competitive

carrier, K uptake will decrease along curve 7. In the absence of an un-competitive carrier, K uptake will decline along curve 8 to the level D, at which K is absorbed mainly by its specific mechanism (exp. 3). The distance between curves 7 and 8 represents uptake of K by the un-competitive carrier.

4.2.4 Application of DONNAN and double-layer theories to K and Mg absorption data

The DONNAN equation
$$\frac{i_K}{\sqrt{i_{Mg}}} = k \frac{M_K}{\sqrt{M_{Mg}}} \quad \text{and}$$

the ERIKSSON type equation
$$\frac{i_K}{i_{Mg}} = k' \frac{M_K}{\sqrt{M_{Mg}}} \quad \text{for}$$

the electric double layer theory presented by BROSHART (1962) did not fit the absorption data for K and Mg obtained in the short-term experiments and the long-term experiment. With decreasing $\frac{M_K}{\sqrt{M_{Mg}}}$ in solution, both k and k' were found to increase. An example in which the data of a short-term experiment were used, was shown in table 8.

The conclusion to be drawn from these findings may be that absorption of both Mg and K by oats involves mechanisms that are too specific to be accounted for by general principles for the equilibria between mono- and divalent cations underlying both DONNAN's and ERIKSSON's approach.

4.3. EFFECT OF pH ON THE ABSORPTION OF MG AND K

In the short-term experiment, Mg absorption took place in the pH range of 3.5 to 9. K uptake started at pH 2.5 and was still continuing at pH 9, the highest level employed (figs. 24a and b). H ions competed with Mg and K for uptake in the ranges of 3.5 to 6 for Mg, and 2.5 to 6 for K. At low pH levels, the oat plant does not seem to possess a mechanism to protect Mg absorption from being disturbed by H ions. In this respect, the oat plant appears to differ from yeast which was reported by CONWAY (1958) to have a specific mechanism for Mg absorption in the pH range of 3.5 to 4.5, that is not affected by H and K. The findings on the effect of the H ions on K uptake are in agreement with the results of FRIED and NOGGLE (1958) for uptake of K by barley roots from solutions with varying pH levels.

Over the pH range of 3 to 9, Mg absorption was suppressed by K, whereas K absorption was promoted by Mg.

In the long-term experiment, with a constant (K + Mg + Ca) concentration in solution, the sum of cations (K + Mg + Ca) absorbed by roots was not affected by changes in solution pH and in nutrient composition but changed with varying solution concentrations. Uptake of Ca and Mg was lower at pH 4 than at pH 6, and, consequently, K uptake was higher at pH 4 than at pH 6. The suppressing effect of H on the uptake of other cations was in the order of Mg, Ca and K.

4.4 EFFECT OF CA ON THE ABSORPTION OF MG AND K

In the short-term experiments 7 and 8, Mg absorption was strongly suppressed by the presence of Ca in the external solution (fig. 25a and 26a). It can, however, not be concluded from these experiments whether or not Ca competes with Mg for identical sites on a common carrier.

From the results of the multiple-regression equation in the long-term experiment, it can be inferred that Mg uptake is not correlated with Ca uptake. This finding agrees with the conclusion drawn by COLLANDER (1941) that Mg distribution between roots and shoots of many plant species is not related in any consistent manner with those of Ca and Sr.

EPSTEIN and LEGGETT (1954), EPSTEIN (1962) and MOORE *et al.* (1961) also found that Ca markedly interferes with the absorption of Mg, but they stated that this interference is not in the nature of competition for identical sites. The latter authors mentioned that Ca may act by altering the structural configuration of the surface groups in such a way as to change their chemical and physical properties.

The suppressing effect of Ca on Mg uptake as found in experiment 8 was smaller than that of K on Mg uptake (fig. 26a). In turn, Ca accumulation was suppressed by Mg in roots, but less so in tops (fig. 25c), whereas it was not suppressed by K in either roots or tops (fig. 26c). The latter finding appears to agree with that of HELMY (1963) who showed that, when the initial content ratio Ca/K in excised barley roots is high, the roots did not absorb Ca unless K was absorbed first, and that at increasing K concentrations both K and Ca were absorbed. On the other hand, Mg was absorbed by plants having low K/Mg ratios.

It is evident from the present experimental results that in many instances plants transferred to a solution medium differing in composition from the original one not only tend to absorb nutrients from the new medium, but also may excrete nutrients into it, especially when the latter differs in nutrient composition from the one originally used. So it was found (fig. 25a) that, when the solution does not contain Ca and Mg and contains K only, the roots excrete Mg into the solution. Likewise, when the solution contained Mg and K (fig. 25c), or Mg only (fig. 26c), the roots excreted Ca and this situation may lead to absorption of Mg in abnormal quantities (fig. 26a) due either to changed characteristics of the root surface or to the absence of an ion competing with Mg for carrier sites and movement into the roots. At moderate concentrations of both Mg and Ca, Mg was absorbed in more normal quantities (fig. 26a) possibly as a result of the presence of a normal root surface, or due to the higher mobility of Ca compared with Mg. Conversely, when the solution contained only K and Ca, Mg was excreted (fig. 25a) and Ca excretion was negligible (fig. 25c).

K absorption from solutions containing K and Mg was not much different from that found in solutions containing Ca as well (figs. 25b and 26b). It might be hypothesized then, that Mg can substitute for Ca in creating a root surface which facilitates a normal uptake of K. In other words, Mg might induce a situation which is quasi-

normal in this sense, that the role of Ca in the absorption of K can be assumed by Mg. Accordingly, an adequate Mg concentration in solution may lead to a normal K uptake. K itself might, however, greatly impede the absorption of Mg, due to the former's greater affinity for carrier sites and higher mobility.

Generally speaking, Mg and Ca were not stable in the plants and were excreted into the solutions when the latter did not contain these elements at the start of the experiment. K was not found to be excreted from plants, not even when the ambient solution did not contain K. It seems that roots excrete Ca only when the composition of the ambient solution deviates from that of a medium considered normal for plant growth. Furthermore, there is evidence that, when the solution contains no Ca, but Mg or polyvalent cations, the roots may absorb these other ions as a substitute for Ca in some physiological function ordinarily performed by Ca.

The stimulation effects of Ca, Mg, and other ions may be viewed in this way that, when a solution contains K only, a part of the Ca in the roots is excreted and roots under this condition cease to function normally. In addition, when a solution contains K and Ca, or K and a polyvalent cation (Li also, according to EPSTEIN, 1960), the roots may function normally or quasi-normally.

In the present short-term experiments, Ca in the ambient solution appeared to be useful mainly in preventing the excretion of Ca absorbed during the pre-experimental period. Ca absorption during the actual experimental period was nil. The presence of Ca in the ambient solution promoted K uptake and suppressed Mg uptake in plants having K/Mg and K/Ca content ratios lower than those found in plants growing under normal conditions.

In the long-term experiment, when the K/Mg ratio in solution was adequate for optimum plant growth, Ca contents in roots were found to be high. When the K/Mg ratio was changed to higher and lower values, the Ca contents in roots tended to decrease along with dry matter yields.

4.5 EFFECT OF PHOSPHATES ON THE ABSORPTION OF MG AND K

In the short-term experiments, Mg uptake by roots from solutions containing phosphates was lower than from those containing chloride (figs. 27a and 28a). Mg uptake via the absorption mechanism common for Mg and K seemed to be particularly impeded by the presence of phosphates in the ambient solution (fig. 28a). It was further found that P was excreted from roots bathed in solutions containing chloride and no phosphates, and that uptake of Mg from these solutions was high. From this, it may be implied that the high rate of Mg absorption from the chloride solution without K is correlated with decreases in P contents of roots, assuming that P in roots exerts some suppressing effect on Mg uptake. This relationship between Mg and P shows similarities with that between Mg and Ca in roots discussed earlier. In

tops, the accumulation of Mg was little affected by changes in anionic species in the nutrient solution (fig. 27a and 28a).

Uptake of K by roots was higher from phosphate than from chloride solutions, when the K concentration in solution was 1 me. (fig. 27b). In tops, K accumulation was larger in chloride than in phosphate solutions (fig. 27b). With increasing K concentrations in solution (fig. 28b) K contents in both roots and tops were higher for chloride than for phosphate solutions having K concentrations exceeding 1 me. K.

According to the results of the multiple-regression equation pertaining to the long-term experiment, Mg in tops was negatively correlated with P. In roots, uptake of both Mg and P appeared to be appreciably affected by the K/Mg ratio in solution and by K uptake (fig. 4). P uptake increase at high levels of K uptake (fig. 4; table 5).

Concerning the absorption of P, experiment 9 (fig. 27c) shows that, when phosphate concentrations increased from 1 to 2 m-moles with increases in Mg from 0 to 1 me., the uptake of P increased very sharply and seemed related more with Mg concentrations than with P concentration in solution. In spite of an initial P/Mg content ratio in roots being lower than found in normal plants P uptake was low at low Mg concentrations in solution. The initial P/Mg content ratio in experiment 9 was 0.43, being lower than the normal value.

In experiment 10 (fig. 28c), in which phosphate concentrations increased from 1 to 11 m-moles with K increasing from 0 to 10 me., the uptake of P again was correlated with K more than with P concentrations in solution. However, in this case, the rate of increase in K uptake was higher than that for P, possibly due to a high initial P/K content ratio of 0.60 in roots, being 4 times as high as found under normal conditions. From the P uptake curves in experiments 9 and 10 (figs. 27c and 28c) it can be implied that K concentration in solution is related less than Mg concentration with P uptake.

In the long-term experiment, in spite of the wide changes in contents of P, as well as of Ca in roots, the contents of these nutrients in tops were not affected by pH, composition and concentration changes in solution (figs. 3, 4, and 5). In contrast, contents of other nutrients in tops were markedly affected by changes in external conditions. This anomalous behavior of P and Ca seems to suggest that the accumulation of these elements in tops is governed by processes taking place inside the plant more than by the condition of the ambient solution.

SUMMARY

Interactions in Mg and K uptake were studied, especially in relation with the following factors affecting ion uptake.

- a. the mechanisms of absorption of both ions involved.
- b. the relationship between absorption of the ions and their concentrations in solution.
- c. the relationship between absorption of the ions and their ratios in the nutrient solution, particularly the ratio of K and Mg in solution.
- d. the effects of H, Ca, N, and P on the absorption of K and Mg.

These factors were examined in a long-term experiment and in short-term experiments. For both types of experiments, use was made of oat plants. The results obtained were tested in connection with two theories on ion absorption, namely the carrier theory and the adsorption theory.

In the former, a combination between free ions and carrier is assumed to be a prerequisite for the active absorption of nutrients. In the latter, adsorption of free ions on an active surface is considered to be the first step in nutrient absorption.

Applying the theories to the data obtained, it appeared that at least two mechanisms were found for the uptake of each ion under investigation. Both Mg and K seem to have a mechanism of uptake that is specific for the ion involved. Uptake via these mechanisms is unaffected by the quantity in which other ions are present in the ambient solution.

The second mechanism via which both ions enter the plant is one that they share. The extent of absorption of both ions via this mechanism is governed by the concentration ratios of these ions and by the degree of affinity between ion and mechanism.

In addition, when applying the carrier theory, evidence was obtained for the existence of a carrier via which both K and Mg can be transported, but which shows a stimulation of K uptake by Mg, implying the presence of un-competitive inhibition of Mg by K.

Both the carrier and the adsorption theory appeared to be useful in explaining the ion absorption phenomena in oats. The possibility of a system whereby an adsorption process precedes the absorption of ions via a carrier system has to be considered, but was not further explored in this study. The mathematics involved in an approach combining the two systems does not differ greatly from those employed in the carrier theory.

The uptake of both K and Mg increased with increasing concentrations of these ions in solution. However, the ratios of the ions absorbed were determined by the composition of the solution, and not by the solution concentration.

In both tops and roots of oat plants grown in the long-term experiment, Mg and K contents were inversely correlated. This antagonism can be explained as competition

for carrier sites common for both ions. Mg absorbed by roots via the mechanism common for Mg and K was not transported into tops in the short-term experiment (17 hours) when plants had low K/Mg content ratios. In the long-term experiment, such transportation proceeded normally.

In the concentration series of the long-term experiment, each having a constant (K + Mg + Ca) concentration, the absorption of K increased, but Mg and Ca decreased with pH levels in solution decreasing from 6 to 4.

Furthermore in the long-term experiment, the sum of cation uptake (K + Mg + Ca) by roots was not affected by solution pH and composition, and varied only with solution concentration. Therefore, low pH levels may be a factor in depressing Mg uptake and increasing the content ratio K/Mg in plants.

The composition of the solution especially the presence of Ca and P appears to be important for normal ion uptake. When the cultural solution contains only a single ion and no Ca and P, the plant may not absorb the ion in a normal manner, and may expel Ca and P. The stimulatory effect and protective effect on selective ion absorption exerted by Ca or polyvalent ions may be simply a restoration of normal conditions of ion uptake, disturbed by imbalance among participating ions. In the present experiments, Mg was found to be able to assume functions normally performed by Ca.

Mg deficiency symptoms developed in the long-term experiment in solutions having K/Mg ratios higher than 9. In this range, Mg is absorbed mostly by its specific mechanism only, and K is absorbed by its specific mechanism as well as by the mechanism common for K and Mg. The severity of the symptoms seemed to be correlated with increases in the Ch-Mg/Mg ratio, and with increases in the K/Mg, Ca/Mg, N/Mg and P/Mg absorption ratios. pH, although affecting the absorption of both Mg and other ions as well as yield of dry matter, had no visible effect on Mg deficiency symptoms.

When Mg in solution is so low, that it can be absorbed only by its specific mechanism, the control of absorption ratios, like K/Mg, Ca/Mg, N/Mg, P/Mg etc., by means of solution composition and the regulation of other metabolic factors, like temperature, light, respiration, etc. may be important factors in preventing Mg deficiency and its symptoms.

When solutions used in the short-term experiments contained $MgCl_2$ only, the uptake of Mg was extraordinarily high and P was excreted from roots. When the solution contained Mg phosphates, Mg uptake was low and P was not excreted from roots.

In the roots which had high P/K and low P/Mg content ratios, P uptake was sharply increased with increases in K and Mg in solution.

SAMENVATTING

Er werd een onderzoek ingesteld naar de opname van Mg en K, speciaal in verband met de volgende factoren:

- a. De absorptiemechanismen van beide ionen.
- b. Het verband tussen de absorptie van deze ionen en hun concentraties in de voedingsoplossing.
- c. Het verband tussen de opname van deze ionen en de chemische samenstelling van de voedingoplossing, in het bijzonder de betekenis van de verhouding van K en Mg.
- d. Het effect van H, Ca, N, en P op de opname van K en Mg.

Deze factoren werden onderzocht in een proef van lange duur (4 weken) en in proeven van korte duur (17 uur). Voor beide soorten proeven werd haver als proefplant gebruikt.

De verkregen resultaten werden getoetst aan twee theorieën, namelijk de „carrier” theorie en de adsorptie theorie. Voor de eerstgenoemde theorie wordt een combinatie tussen vrije ionen en een „carrier” als noodzakelijke voorwaarde gesteld voor het plaatsvinden van actieve ionenopname. In de tweede theorie wordt adsorptie van vrije ionen aan een actief oppervlak gezien als een eerste stap in het opnameproces.

Bij het toepassen van de wiskundige formuleringen van de genoemde theorieën op de experimenteel verkregen gegevens bleek dat tenminste twee opnamemechanismen voor beide ionen aanwezig zijn. Zowel Mg als K bezit een opnamemechanisme dat specifiek is voor het betreffende ion. Opname via zulk een mechanisme wordt niet beïnvloed door de aanwezigheid van andere ionen in de voedingsoplossing.

Het tweede mechanisme waarmee K en Mg door de plant kunnen worden opgenomen is een gemeenschappelijk systeem. De mate waarin de ionen via dit mechanisme worden geabsorbeerd is afhankelijk van hun concentratieverhouding in de oplossing en van hun respectievelijke affiniteiten voor het mechanisme.

Verder bleek bij toepassing van de „carrier” theorie dat nog een „carrier” aanwezig is welke zowel Mg als K kan transporteren. Via deze carrier wordt echter de opname van K gestimuleerd door de aanwezigheid van Mg, hetgeen wijst op het voorkomen van „un-competitive inhibition”.

Zowel de carrier- als de adsorptietheorie bleken van nut te zijn bij het verklaren van de ionenopname bij haver. Met de mogelijkheid van het bestaan van een systeem waarbij een adsorptieproces aan de opname van ionen via een „carrier” voorafgaat, moet rekening gehouden worden. In deze studie werd hier echter verder geen aandacht aan besteed, aangezien de wiskundige benadering van zo’n systeem sterke overeenkomst vertoont met de formulering welke gebruikt werd voor de „carrier” theorie.

De opname van zowel K als Mg nam toe met toename van de concentratie van de ionen in de voedingsoplossing. De verhouding, waarin de ionen werden opgenomen, werd echter bepaald door de samenstelling en niet door de concentratie van de oplossing.

In zowel de bovengrondse delen als de wortels van de haverplanten in de proef van lange duur waren de Mg en K gehalten negatief gecorreleerd. Dit antagonisme kan verklaard worden als zijnde concurrentie voor plaatsen aan de carrier welke Mg en K delen. Mg dat was opgenomen door de wortels via het gemeenschappelijke mechanisme bleek in de korte-duur opnameproeven (17 uur) niet getransporteerd te worden naar de bovengrondse delen van planten met een lage K/Mg verhouding. In de proef van lange duur vond dit transport normaal plaats.

In de concentratieseries van de proef van lange duur, elk met een constante (K + Mg + Ca) concentratie, nam met verlaging van de pH in de oplossing van 6 tot 4 de opname van K toe en die van Mg en Ca af. Verder bleek in de proef van lange duur de som van de kationenopname (K + Mg + Ca) niet te worden beïnvloed door de pH en de samenstelling van de voedingsoplossing. Deze som varieerde alleen met de totale concentratie van kationen in de oplossing. Lage pH waarden kunnen derhalve oorzaak zijn van onvoldoende Mg opname en een te hoge verhouding van K tot Mg in de plant.

De samenstelling van de voedingsoplossing en speciaal de aanwezigheid van Ca en P blijkt van belang te zijn voor een normaal verlopende ionenopname. Als de oplossing slechts één ion bevat en geen Ca en P, bestaat de mogelijkheid dat dit ion niet normaal wordt opgenomen en dat Ca en P door de plantenwortel worden afgescheiden. Het stimulerende effect en het beschermende effect op de selectieve ionenabsorptie dat uitgeoefend wordt door Ca en andere meerwaardige ionen kan dus eenvoudig zijn een herstel van de normale toestand die verstoord werd door een onevenredige verdeling van ionen die deelnamen aan het absorptieproces. In de huidige proeven werd gevonden dat Mg functies kan vervullen, die gewoonlijk door Ca worden verricht.

Mg gebreksverschijnselen ontwikkelden zich in de proef van lange duur in oplossingen met K/Mg verhoudingen hoger dan 9. Boven deze verhouding wordt Mg voornamelijk opgenomen via het specifieke mechanisme. K opname verloopt dan zowel via het specifieke als het gemeenschappelijke mechanisme. De mate van gebreksverschijnselen schijnt in verband te staan met toename in de verhouding van chlorophyll-Mg tot totaal Mg en met toename in de K/Mg, Ca/Mg, N/Mg en P/Mg opnameverhoudingen. pH verschillen, hoewel van invloed op de opname van Mg en andere ionen als ook op de droge-stof opbrengst oefenden geen waarneembare invloed uit op de mate van Mg gebreksverschijnselen.

Als de Mg concentratie in de voedingsoplossing zo laag wordt, dat het ion alleen via het voor Mg specifieke mechanisme wordt opgenomen kunnen factoren, zoals het beheersen van opnameverhoudingen (K/Mg, Ca/Mg, N/Mg, P/Mg, etc.) door middel van de samenstelling van de voedingsoplossing, en het regelen van temperatuur,

licht, ademhaling e.d. van belang zijn voor het voorkomen van Mg gebrek en de verschijnselen, die daarvan het gevolg zijn.

Wanneer de voedingsoplossingen in de opnameproeven van korte duur $MgCl_2$ bevatte, was de opname van Mg uitzonderlijk hoog en werd P door de wortels afgescheiden. Bij de aanwezigheid van alleen Mg fosfaten in de oplossing was de Mg opname gering en werd P niet afgescheiden.

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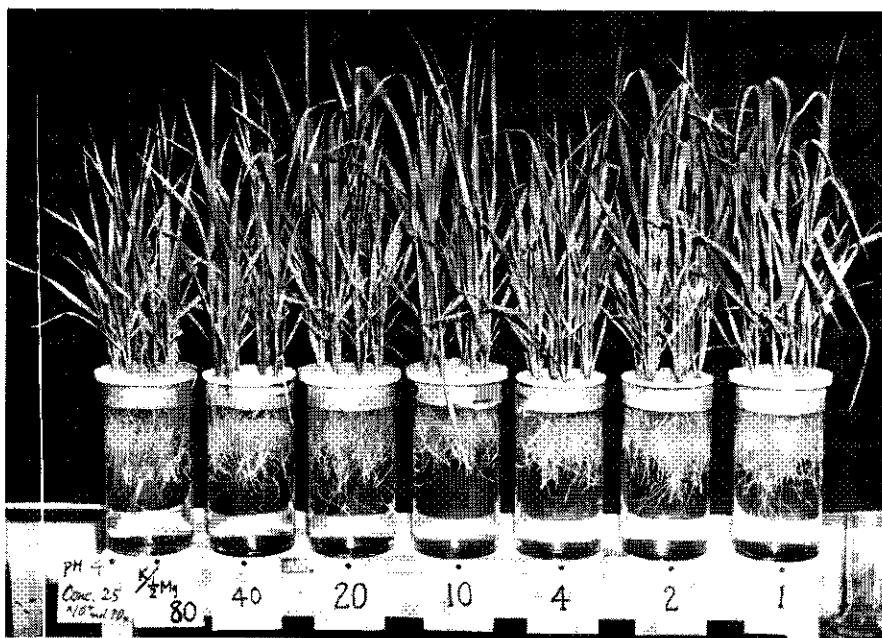


PHOTO 1. Oats in the K/Mg ratios 80, 40, 20, 10, 4, 2 and 1 at a concentration of 2.5 me. (K + Mg) per liter at pH 4, 24 days after transplanting.

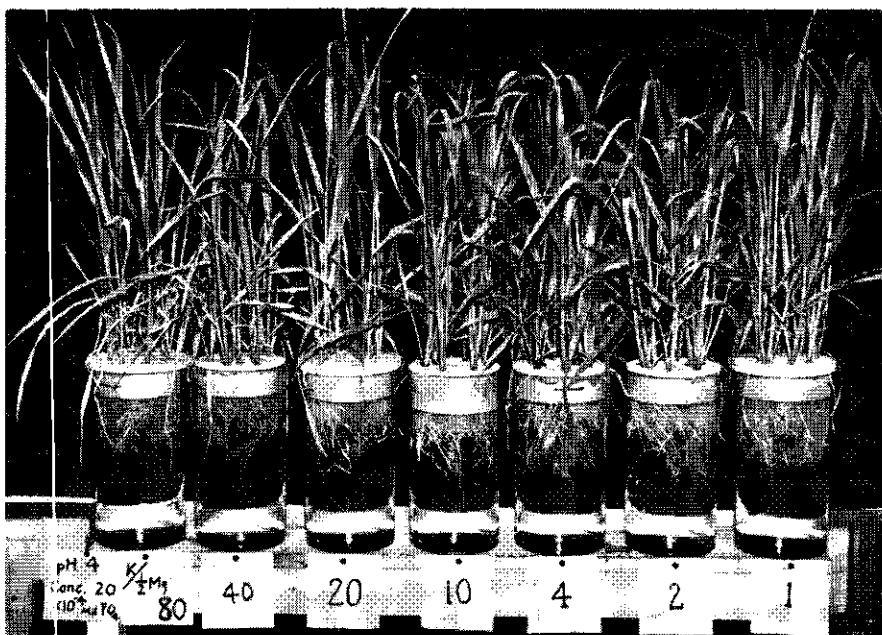


PHOTO 2. Oats in the K/Mg ratios 80, 40, 20, 10, 4, 2 and 1 at a concentration of 20 me. (K + Mg) per liter at pH 4, 24 days after transplanting.

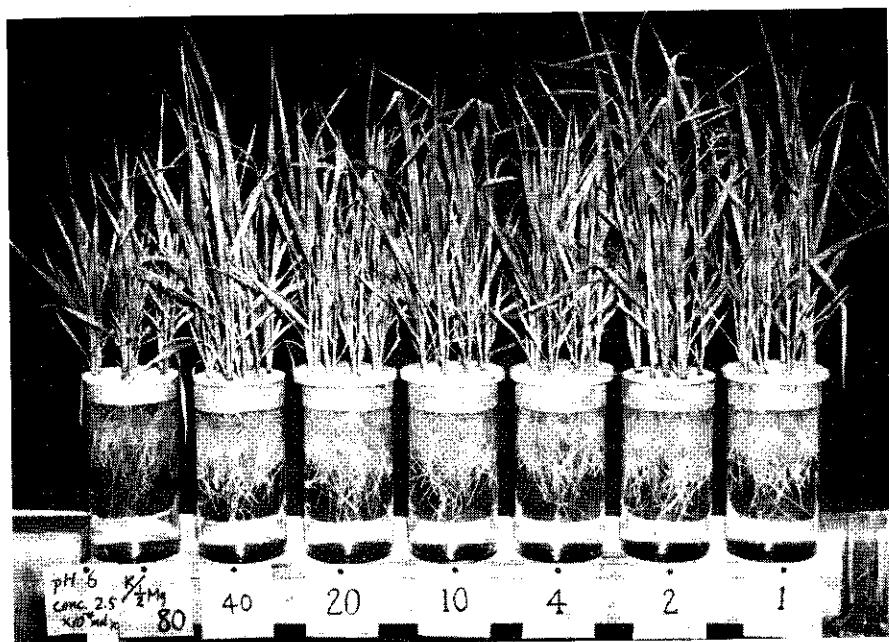


PHOTO 3. Oats in the K/Mg ratios 80, 40, 20, 10, 4, 2 and 1 at a concentration of 2.5 me. (K + Mg) per liter at pH 6, 24 days after transplanting.

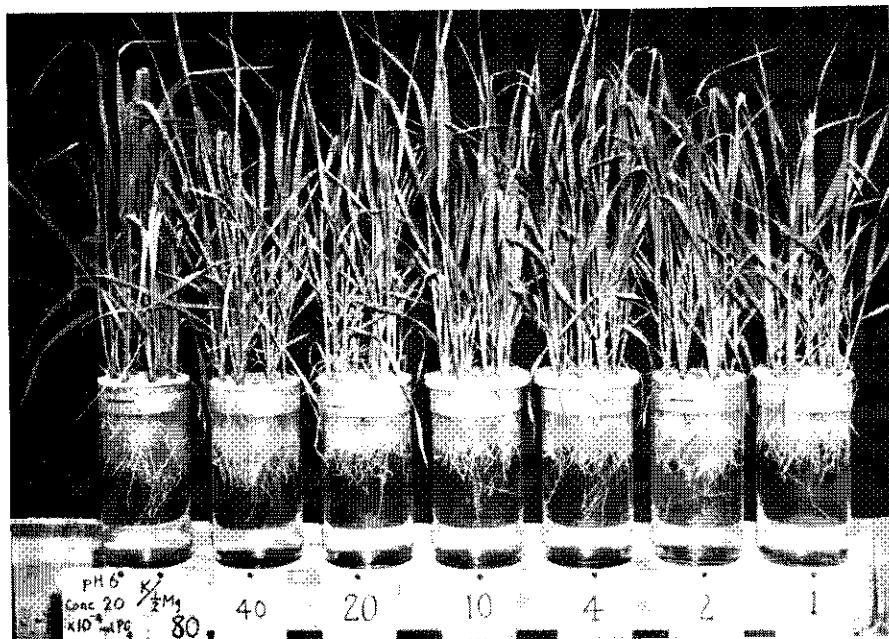


PHOTO 4. Oats in the K/Mg ratios 80, 40, 20, 10, 4, 2 and 1 at a concentration of 20 me. (K + Mg) per liter at pH 6, 24 days after transplanting.



PHOTO 5. Oats in the concentrations 2.5, 5, 10 and 20 me. (K + Mg) per liter for the K/Mg ratio of 20 at pH 4 and 6, respectively, 24 days after transplanting.



PHOTO 6. Oats at pH levels of 4, 5 and 6 for the K/Mg ratio of 20 at concentrations of 2.5 and 20 me. (K + Mg) per liter, 24 days after transplanting.

APPENDIX. Results of the long-term experiment on the influences of pH, K/Mg ratio and concentration of solution on yield of dry matter and of nutrients in oat plants

pH 4				Yield of dry matter ¹				K ²				Mg				Ch-Mg ³				Ca				N				P			
K/Mg ratio in solution	(K + Mg) in me. per liter	T ⁴	R	Tops	Roots	T	R	T	R	T	R	T	R	T	R	T	R	T	R	T	R	T	R	T	R	T	R	T	R		
79	2.5	5.8	1.2	4.83	218	195	1.1	3.4	1.75	23.4	9.0	298	282	25.3	32.8	5	5.8	1.4	4.14	211	187	1.8	5.1	23.0	9.6	280	287	26.2	32.6		
5	4.0	1.0	4.00	208	166	2.6	4.5	2.05	19.4	9.6	296	283	22.4	27.6	4.8	1.2	4.00	211	127	2.2	21.0	9.1	315	224	25.8	23.4					
10	4.9	1.1	4.45	220	172	1.5	4.6	1.78	18.6	11.0	322	297	24.3	35.2	5.5	1.2	4.58	229	125	1.9	3.0	18.4	10.0	322	241	23.3	26.4				
20	5.3	1.1	4.82	231	202	1.6	4.9	2.27	21.5	15.9	304	286	25.1	44.0	4.0	0.9	4.44	255	218	2.2	4.1	22.8	13.5	339	282	27.4	40.4				
39	2.5	6.0	1.7	3.53	167	140	1.6	1.6	2.10	21.3	8.0	277	254	26.4	24.4	5.4	1.2	4.50	179	172	1.8	3.3	21.3	9.5	281	274	22.6	29.3			
5	5.7	1.2	4.75	208	179	2.1	5.0	2.64	23.0	9.0	320	291	24.4	29.8	7.0	1.4	5.00	196	176	2.8	5.7	22.5	10.3	317	289	24.2	32.4				
10	7.1	1.5	4.73	216	190	2.6	6.2	2.37	18.2	10.5	326	287	24.1	32.4	7.4	1.5	4.93	219	142	2.2	7.5	18.9	15.0	336	307	23.3	40.4				
20	5.1	1.2	4.25	211	167	1.8	3.4	2.50	19.3	13.1	328	275	26.7	39.8	5.0	1.1	4.55	240	189	2.1	2.0	27.2	17.0	334	274	27.1	38.8				
19	2.5	5.5	1.3	4.23	183	177	2.9	6.3	2.93	23.8	10.0	296	276	25.0	34.0	5.9	1.4	4.21	185	160	2.9	4.6	20.8	9.1	282	275	26.1	33.0			
5	5.8	1.3	4.46	167	134	2.6	5.3	2.65	20.0	9.8	291	246	22.8	28.4	6.8	1.6	4.25	188	154	2.4	5.1	20.4	9.0	306	246	26.1	27.2				
10	6.3	1.3	4.85	204	162	3.5	5.8	3.02	20.1	9.1	316	277	23.3	31.6	6.4	1.3	4.92	198	136	3.0	3.6	17.2	11.0	316	242	25.5	33.4				
20	6.8	1.6	4.25	197	182	2.1	5.5	2.99	17.7	20.1	303	294	25.4	40.0	5.4	1.4	5.21	206	144	3.4	4.0	23.1	17.3	314	253	25.4	30.6				
9	2.5	5.4	1.4	3.86	158	138	4.4	6.2	2.88	25.0	10.0	310	232	23.8	23.4	5.9	1.5	3.93	165	154	3.8	5.4	24.7	8.0	295	248	23.7	27.2			
5	7.1	1.5	4.73	179	167	3.6	5.8	2.73	23.0	11.6	319	285	25.8	29.6	6.3	1.3	5.00	169	147	3.7	2.8	20.8	11.6	319	285	23.0	31.1				

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Yield of dry matter in grams per culture	120
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K, Mg, Ca, and N in me. per 100 g dry matter; P in m-moles per 100 g dry m-

pH 6 K/Mg ratio in solution	(K + Mg) in me. per liter	Yield of dry matter				Tops				K				Mg				Ch-Mg				Ca				N				P																																																																																																																																																																																																																																																																																																																																																																																																																											
		T		R		Roots		T		R		T		R		T		R		T		R		T		R		T		R																																																																																																																																																																																																																																																																																																																																																																																																																											
		79	2.5	4.5	1.2	3.75	183	152	2.8	5.9	2.33	26.0	8.5	297	268	25.7	38.6	5	6.7	1.4	4.79	195	150	1.7	3.6	1.98	17.4	10.6	306	227	23.6	26.6	6.0	1.5	4.00	178	183	1.7	6.4	16.7	10.3	264	333	25.2	26.0	6.6	1.4	5.00	200	179	2.1	6.1	1.82	19.3	13.3	323	296	25.6	34.8	7.0	1.4	5.07	200	169	2.0	6.3	1.89	17.5	14.6	322	279	26.5	32.8	7.1	1.4	5.29	207	198	2.0	7.4	1.89	17.2	22.2	321	309	23.2	44.5	7.4	1.4	4.71	212	168	2.0	6.8	19.6	26.6	340	269	25.8	44.6	6.6	1.4	4.71	212	168	2.0	6.8	19.6	26.6	340	269	25.8	44.6	39	2.5	5.6	1.5	3.73	200	169	2.4	4.6	2.41	25.2	10.0	313	267	26.0	29.0	6.1	1.5	4.07	182	156	2.8	5.0	21.0	9.9	277	255	22.4	27.0	5.8	1.6	3.63	185	162	2.1	4.9	2.20	19.3	9.4	295	283	25.8	36.0	6.9	1.5	4.60	183	169	2.4	5.9	2.28	16.5	12.1	316	288	25.5	40.4	7.1	1.5	4.73	183	169	2.4	5.9	2.28	16.5	12.1	316	288	25.5	40.4	7.0	1.6	4.38	198	162	2.6	5.6	22.1	11.2	334	284	26.7	32.6	7.4	1.4	5.29	212	177	2.8	6.8	2.58	15.8	24.0	335	289	25.2	38.8	6.6	1.4	4.71	210	179	2.8	8.0	18.7	27.1	320	313	25.6	46.3	19	2.5	5.9	1.6	3.69	163	147	2.3	5.6	3.21	22.8	9.6	272	256	24.0	26.4	5.9	1.5	3.93	172	142	3.0	6.7	21.6	10.1	278	260	23.0	27.2	6.2	1.5	4.13	193	173	3.1	8.3	3.44	20.3	9.6	308	282	24.4	29.6	6.4	1.6	4.00	180	177	2.1	7.0	20.0	11.5	307	268	24.4	28.0	8.6	1.8	4.78	187	149	2.7	7.4	3.44	20.0	16.6	305	244	25.6	30.4	8.4	1.8	4.67	193	186	2.4	9.0	22.8	17.2	325	287	26.4	37.0	7.3	1.5	4.86	199	141	3.2	7.6	3.47	23.7	25.0	350	258	29.8	39.2	8.3	1.7	4.88	210	157	3.4	8.6	17.7	23.6	333	243	24.7	34.8	9	2.5	5.8	1.6	3.63	182	129	4.1	5.7	3.09	25.0	10.0	297	238	29.2	23.8	6.2	1.8	3.44	173	137	4.6	6.3	18.6	9.0	287	238	21.4	21.2	7.2	1.9	3.79	179	151	3.8	7.8	3.29	20.4	11.5	316	264	24.9	27.6	6.9	1.5	4.60	168	112	3.7	8.0	21.4	10.2	303	221	23.3	19.4	7.9	1.7	4.64	185	140	3.5	11.9	3.30	18.9	21.8	318	272	24.6	17.4	8.4	2.2	3.82	172	151	3.6	12.7	21.6	16.4	324	267	30.6	24.0	20	8.8	2.2	4.00	196	156	3.4	12.3	3.21	20.4	52.8	342	259	32.0	29.0	8.4	1.7	4.94	187	139	3.9	8.2	139	21.0

4	2.5	5.7	1.6	3.56	155	126	4.9	8.3	2.93	23.4	8.8	287	237	23.8	20.8
		6.1	1.5	4.07	145	148	4.8	9.4	2.8	22.8	9.2	268	253	22.0	26.4
5	5	6.7	1.6	4.19	140	115	5.0	11.2	2.64	19.8	9.3	280	249	25.1	21.2
10	10	7.4	1.7	4.35	146	135	4.6	11.3	18.7	11.9	276	266	22.9	22.6	
20	20	8.7	1.7	5.12	173	152	5.4	14.8	2.75	17.4	15.5	323	283	23.0	25.8
		8.6	2.1	4.10	185	150	7.2	12.2	2.32	20.0	346	289	28.0	27.2	
1	2	9.1	1.9	4.79	176	145	7.1	15.9	2.71	20.7	59.4	325	25.3	50.2	
		8.9	1.7	5.24	179	161	6.8	17.1	20.8	37.4	312	272	25.0	21.0	
2	2.5	6.8	1.8	3.78	142	124	7.3	13.2	2.30	17.5	9.6	260	229	20.2	20.2
		6.9	1.8	3.83	146	106	7.0	9.1	2.47	17.9	8.1	268	184	20.0	15.2
5	5	7.7	1.7	4.53	158	130	6.4	18.0	2.47	17.9	11.6	314	270	23.4	26.2
10	10	6.7	1.6	4.19	134	123	5.7	10.7	18.7	8.6	292	237	21.8	21.0	
20	20	8.7	1.7	5.12	182	139	7.3	20.8	2.74	20.4	28.0	311	264	25.8	31.2
		8.0	1.9	4.21	169	130	7.9	21.1	21.8	18.6	337	251	30.6	27.4	
1	2	8.4	1.7	4.94	169	148	7.7	17.0	2.64	20.0	29.9	323	280	25.4	38.8
		7.9	1.7	4.65	183	153	10.4	16.0	25.0	36.6	333	268	26.3	38.8	
1	2.5	6.8	1.6	4.25	148	118	7.3	16.6	2.35	19.6	10.6	276	230	22.4	20.6
		5.9	1.5	3.93	156	103	7.7	13.0	18.6	8.0	267	222	20.8	17.8	
5	5	7.7	1.7	4.53	173	115	9.3	19.9	2.48	18.7	9.8	306	235	21.7	16.8
10	10	7.7	1.9	4.05	148	105	9.1	24.1	21.1	18.4	296	239	26.0	18.8	
20	20	8.2	1.5	5.07	181	134	9.1	21.9	2.83	17.5	12.4	317	268	24.9	26.6
		8.6	1.7	5.47	150	122	10.5	16.9	3.01	20.4	20.3	337	284	26.4	26.0
		8.6	1.7	5.06	165	121	17.5	18.5	24.0	30.7	333	254	26.7	28.4	
									40.2	40.2	331	257	27.2	36.8	