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An investigation of Mn uptake by five-day-old excised barley roots revealed that a metabolically-mediated process was involved. In short-term experiments, the rate of Mn absorption was comparable to that of the macronutrient cations. Like other metabolically absorbed cations, the Mn absorption rate was a direct function of the ambient concentration and the pH.

An evaluation of mutual effects between Mn and other cations revealed several specific regulatory effects. Of the alkali cations studied, Li alone had a pronounced stimulatory effect while Na, K and Rb markedly reduced the absorption of Mn. The alkaline earth cations also exerted widely differing effects. Calcium appeared to promote the absorption of Mn, whereas Mg had a highly inhibitive effect. The combination of both Ca and Mg was even more inhibitory. Strontium apparently was without effect and Ba had a moderately depressive effect. Other polyvalent cations which were effective inhibitors of Mn absorption were Fe^{++}, Zn, Cu, Al and La. In

contrast, Fe^{+++} was virtually without effect. Manganese effectively blocked the absorption of Li and Mg, but greatly enhanced that of Na, K and Rb.

These diverse regulatory effects and many others reported in the literature are explained by the following hypothesis: the cationic environment at the extracellular surface of the membrane is believed to control the specificity of the ion carrier. By attaching to critical activation sites, cations induce conformational changes in the carrier which modify its selective transport properties. The accessibility or affinity of transport sites for a given ion would depend on the particular configuration of the carrier. This mechanism, together with the mutual competition between some ions for the same transport site and the cationic maintenance of the cellular membranes, would explain most, if not all, of the regulatory effects exerted by cations on the ion absorption process.

MANGANESE ABSORPTION BY BARLEY ROOTS

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INTRODUCTION

Although numerous investigations of ion absorption by plant tissues have been conducted, relatively little attention has been given to Mn. In view of the selectivity and differential transport of cell membranes, it behooves us to understand and characterize the absorption of all ions. The importance of investigating Mn absorption is intensified knowing its essentiality to plant metabolism and the problems of Mn deficiency and toxicity. Considerable literature exists on the general nutrition of Mn. Plant deficiencies, toxicities and functions of Mn have been reviewed recently by several authors (Hewitt, 1963; Jackson, In press; Nason and McElroy, 1963).

The uptake and translocation of Mn by intact plants from soil or complete nutrient solutions has received extensive attention. The reader is referred to an excellent and current review of this subject by Jackson (In press). Investigations of this type reveal a great deal about the availability of Mn, its distribution within plants and the interrelationships with other elements. However, little information can be obtained regarding the absorption mechanism, per se. The use of intact plants growing in either soil or complete nutrient solutions inherently involves a complex system with many uncontrolled and unknown variables.

Only experiments which have dealt with the uptake of Mn by relatively simple plant tissues under controlled experimental conditions will be considered here. A few exceptions, where pertinent, are included. Studies at the cellular level with single-salt solutions or controlled salt-mixtures should provide more definite information about ion absorption.

The earliest known study of Mn uptake by excised root tissue was made by Laine (1934) with decapitated roots of Phaseolus multiflorus. Analyses of both the exudate and the roots revealed an accumulation and retention of Mn by the roots. Roots immersed in a 10^{-5} N $MnCl_2$ solution absorbed essentially all of the ambient Mn. However, only 3.5% was detected in the exudate. When placed in distilled water for three weeks, 80% of the Mn was retained by the detached roots. Laine questioned whether this apparently insoluble Mn was simply precipitation of Mn as Lundegardh (1932) had suggested earlier.

Using carrot tissue slices, Stiles and Skelding (1940) studied Mn uptake from solutions ranging in concentration from 0.02 to 0.0002 M. They observed that the uptake of Mn occurred in two distinct phases. An initial phase of rapid uptake was followed by an extended period of comparatively slower absorption. The time course of Mn uptake was essentially the same from chloride, nitrate or sulfate salts. In general, equivalent amounts of Mn were

absorbed from chloride and nitrate solutions while that absorbed from the sulfate was less.

Results comparable to those found with carrot slices were also obtained with other storage tissues such as red beet, swede, mangold, artichoke and parsnip (Stiles and Dent, 1946; Rees, 1949). The two-phase course of uptake reported by these investigators is characteristic of the ion uptake process. The usual interpretation given to the two phases is that the first is a non-metabolic, passive process, whereas the second is dependent upon respiratory metabolism (Laties, 1959). Unfortunately, the metabolic dependence of the two phases of Mn uptake was undetermined by the above authors. However, observations by Rees (1949) of the effects of conditions during tissue preparation on the subsequent absorption of Mn suggested the involvement of metabolism. Absorption appeared to be materially affected by such pretreatment variables as temperature, aeration and extent of washing.

In subsequent experiments with red beet discs, Skelding and Rees (1952) confirmed that the first phase was a physical process and the second was physiological. They found that absorption during phase two could be essentially eliminated at a temperature of 1^{o} C or by prolonged treatment with nitrogen. In contrast, the uptake during phase one was little affected by temperature or anoxia. Considerable interest was also focused on the inhibition of Mn

absorption by an aqueous extract from the beet roots. They proposed that the lag period in salt absorption by the storage tissue was associated with some internal inhibitor. Later it was shown that carbon dioxide also depressed the absorption of Mn (Skelding, 1957). From these results it was hypothesized that the inhibitory substance was formed by dark fixation of respiratory carbon dioxide.

The interpretation of these results, however, was not supported by Dale and Sutcliffe (1959). The effect of carbon dioxide was not questioned, but the existence of an internal inhibitor of salt accumulation was seriously doubted. Their investigations revealed differential effects of the beet-root extract on K and Mn absorption. The inhibition of Mn absorption was attributed rather, to the chelating properties of the beet extract. They suggested that formation of Mn-complexes simply reduced the availability of Mn in the ambient solution. The controversy appeared to terminate at this point as no further publications on the uptake of Mn by these investigators was found.

The uptake of Mn by algae (Harvey, 1947; Pollard and Smith, 1951; Knauss and Porter, 1954) has been reported to be very rapid, though in each case only physical adsorption was believed to be involved. A similar conclusion was made by Roberts and Aldous (1951) after studying the uptake of Mn by Escherichia coli. They believed that Mn was adsorbed on proteins or nucleic acids in a

loosely bound complex. The amount adsorbed was considered a function of the concentration of Mn and competing ions and the number of available adsorption sites. On the other hand, Rothstein and associates (Rothstein, et al., 1958; Jennings, Hooper and Rothstein, 1958) have demonstrated that active transport of Mn occurred in yeast cells in the presence of glucose and phosphate. They found that the absorption mechanism was highly selective for Mg and Mn and independent of adsorption on the cell surface. The requirement for phosphate absorption preceding or concomitant with Mn absorption suggested the participation of phosphate in the synthesis of a Mn and Mg carrier. A very simplified scheme was presented to account for their observations of the metabolic transport of Mn and phosphate.

Digressing from plant-nutrient investigations for a moment, a study of Mn absorption by human red blood cells has led to the conclusion that uptake was a purely passive process (Weed and Rothstein, 1960). These results are open to question, however, because the experiments were conducted at pH 7.4. This condition is highly conducive to rapid oxidation and precipitation of Mn. Chappell and associates (Chappell, Greville and Bicknell, 1962; Chappell, Cohn and Greville, 1963), on the other hand, have found that rat liver mitochondria accumulated Mn. Furthermore, they reported that the uptake of Mn was accompanied by an increased

rate of respiration and that both processes could be inhibited by such metabolic poisons as cyanide, dinitrophenol and antimycin.

Although the observations by Munns, Jacobson and Johnson (1963) on Mn uptake were made from complete nutrient solutions, reference to their work seems relevant to this discussion. In experiments with intact and excised oat roots, they found three distinguishable fractions of Mn in the roots. These fractions were termed "replaceable," "labile" and "nonlabile" based on their exchangeability with substrate Mn and translocation to the shoot. The replaceable Mn was defined as that fraction which could be removed rapidly by electrolyte solutions. That Mn retained by the root was further separated into two fractions differentiated on the basis of their lability of movement. The labile Mn equilibrated rapidly with the ambient solution and moved readily to the shoot. Equilibration between the nonlabile Mn and the ambient solution occurred slowly and this fraction was relatively immobile. Although it appears likely that the nonreplaceable fraction may have been metabolically absorbed, the authors did not present data to support this possibility.

Brown and Jones (1962) have studied the uptake of Mn and several other ions with respect to the reductive capacity of soybean roots. The reductive capacity was ascertained by measuring the reduction of ferricyanide-ferrichloride solutions to ferrocyanide by

iron-deficient roots. Uptake was determined with various combinations of single-salt solutions and complete nutrient solutions by detached and attached roots. Approximately equal amounts of Mn were absorbed by excised and intact roots. A positive correlation was found between Mn and Fe uptake and the reductive capacity of the roots. Reduction at the root was suggested as a possible factor affecting availability irrespective of the absorption mechanism.

Recently, Page and Dainty (1964) have reported that the uptake of Mn by four-week-old excised oat roots was non-metabolic. This conclusion was based on the results of low-temperature studies and pre-treatments with potassium cyanide and chloroform. Both the characteristic rapid-initial uptake and the following slower steady-state uptake occurred independently of metabolic activity. Similar results were obtained for the time-course of uptake for ambient concentrations of 10^{-7} to 3×10^{-4} M. Uptake in both phases was considered to involve exchange sites which differ only in their accessibility or chemical nature. The zone of greatest uptake was shown earlier by Page (1961) to be the meristematic region. It is of interest that the uptake of Na, Ca, Sr and Cl by the meristematic region of corn roots has also been reported to be non-metabolic (Handley and Overstreet, 1961, 1963; Handley, Vidal and Overstreet, 1960). However, absorption of these ions by the vacuolated tissue was dependent on aerobic metabolism.

In direct contrast to the results of Page and Dainty (1964), Mn absorption by six-day-old excised wheat roots has been found to be metabolically mediated.[1] This conclusion was based on the inhibition of the steady-state Mn absorption by 2,4-dinitrophenol, a commonly used inhibitor of ion accumulation.

This very inadequate knowledge of the nature of Mn absorption under controlled laboratory conditions prompted the initiation of the present study. The purpose of this investigation was to study the nature of Mn uptake by excised barley roots. Specific objectives were:

(1) to determine the metabolic dependence of Mn uptake,

(2) to study the effects of pH, ambient concentration and competing cations on Mn absorption and

(3) to study the influence of various monovalent, divalent and trivalent cations on the absorption of Mn.

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[1] Unpublished data of W. Campbell, D. L. Craig and W. A. Jackson, 1960, reported by Jackson (In press).

MATERIALS AND METHODS

The experimental procedures followed for the growth and preparation of the root tissue and for the conduct of the experiments are described in the following sections. Although several minor modifications have been made, essentially all of the methods used have been patterned after those of Jacobson, et al. (1961a).

Growth of Root Material

One hundred grams of barley seed (Hordeum vulgare L., var. Trebi) were rinsed with distilled water and were germinated by soaking in continuously-aerated distilled water for 24 hours. The germinated seed were again rinsed and spread uniformly on cheesecloth-covered stainless steel racks (8 1/2 x 13 x 2" high). The racks were placed in fiberglass animal cages (9 1/2 x 18 x 5" high) containing three liters of culture solution, which was 0.1 millimolar in $Ca(NO_3)_2$, KH_2PO_4 and $MgSO_4$. Another piece of cheesecloth was spread over the seed with the ends dipping into the solution. To prevent excessive evaporation, a piece of plate glass was placed over the cages. The solutions were aerated throughout the growing period by means of perforated tygon tubing. On the third day after placing the seed on the cheesecloth, the culture solution was replaced with fresh solution. Plants were germinated and grown in

continuous darkness at a controlled temperature of 25± 1° C.

Preparation of Root Material

On the fifth day after the seeds began soaking, the roots were excised just below the seeds. Roots between 8 and 12 centimeters long were obtained at this time. The excised roots were cut into approximately one centimeter lengths and washed several times in distilled water. During the washing, the root material was mixed thoroughly to obtain a homogeneous mass of tissue. Excess water was removed by spinning at 65 x gravity for five minutes in an International centrifuge equipped with a perforated stainless steel basket. Subsequent loss of moisure prior to immersion into the treatment solutions was minimized by covering the root material with dampened cheesecloth spun-dry with the roots.

Experimental Procedure

Seven grams (fresh weight) of root material, weighed on a torsion balance, were immersed in seven liters of test solution. A root to solution ratio of one gram per liter was employed to minimize changes in composition and concentration of the solution during the absorption period (Jacobson, et al., 1961b).

Manganese and all other ions were provided in the treatment solutions as chloride salts. Unless stated otherwise, analyzed

reagent-grade chemicals and distilled water were utilized in all experiments. Glassware and solution bottles were acid washed in 0.5 N HCl and rinsed with distilled water prior to all experiments.

Except where noted, the solutions were aerated continuously, the temperature was maintained at 25° C and the pH at five. Aeration was provided by conducting a stream of filtered, compressed air through the solution by means of heavy-walled glass tubing (2 mm I. D.). The temperature was controlled by placing the bottles in a thermostatically-controlled water bath. The pH was maintained at the desired value by periodic adjustment. When required, reductions in pH were made with additions of 0.1 N HCl. To adjust the pH upward, nylon bags containing analytical grade Bio-Rad AG1-X8 anion exchange resin in OH^- form were dipped into the solution (Parr and Norman, 1963). Changes in the chloride concentration of the treatment solutions, resulting from additions of HCl or from adsorption on the anionic exchange resin, were minor except at pH values below five and above six.

At the end of the absorption period, the roots were collected on a fine-mesh nylon screen and washed by pouring three liters of distilled water over them. Considerable care was taken to standardize the washing procedure from sample to sample. The root material was then placed in 125 milliliter Erlenmeyer flasks and dried overnight at 65 - 70° C.

Chemical Analyses

The oven-dry root material was digested with eight milliliters of nitric and five milliliters of perchloric acids for ten minutes beyond clearing time. The clear digest solution was transferred to 100 milliliter volumetric flasks and brought to volume with re-distilled water. Further dilutions, if required, were made and manganese, iron, copper, zinc, calcium, magnesium and aluminum were determined on a Perkin-Elmer Model 303 atomic absorption spectrophotometer. Calcium and magnesium analyses were made from solutions containing 1500 ppm of strontium. Strontium has been reported to satisfactorily suppress any interferences from aluminum, phosphate, silicate and sulfate (David, 1960). A nitrous oxide-acetylene flame was used in the determination of aluminum. Analyses of lithium, sodium, potassium and rubidium were made on a Beckman Model DU flame emission spectrophotometer.

Respiration Measurements

Oxygen uptake was determined in a Warburg respirometer according to standard manometric techniques (Umbriet, Burris and Stauffer, 1964). Respiration of one-half gram samples of excised root tissue in distilled water was measured over a period of two hours. The temperature was maintained at 30° C.

RESULTS AND DISCUSSION

Basic Characteristics of Manganese Uptake

Manganese Uptake as a Function of Time

The initial experiment was designed to study the course of Mn uptake over a period of several hours (see Appendix Table 1).[2] A single-salt solution, 5×10^{-5} N $MnCl_2$, was deliberately selected so that uptake could be measured exclusive of the effect of other ions. Manganese content of the root material was determined initially and at various intervals up to ten hours following immersion in the test solution. The results are illustrated graphically in Figure 1. Following a rapid initial uptake, Mn was absorbed at a steady-state rate for at least ten hours. This time curve for Mn uptake is very similar to the commonly recognized two-phase ion uptake process. The magnitude and duration of the initial hyperbolic phase of uptake, as defined by Laties (1959), were 1.6 meq per kilogram and 30 minutes, respectively. On the basis of the similarity between the course of uptake of Mn and other cations, the initial phase was considered to be essentially non-metabolic. It must be recognized, of

[2] Complete information regarding the experimental conditions, treatments and results of this and subsequent experiments is tabulated in the appendix.

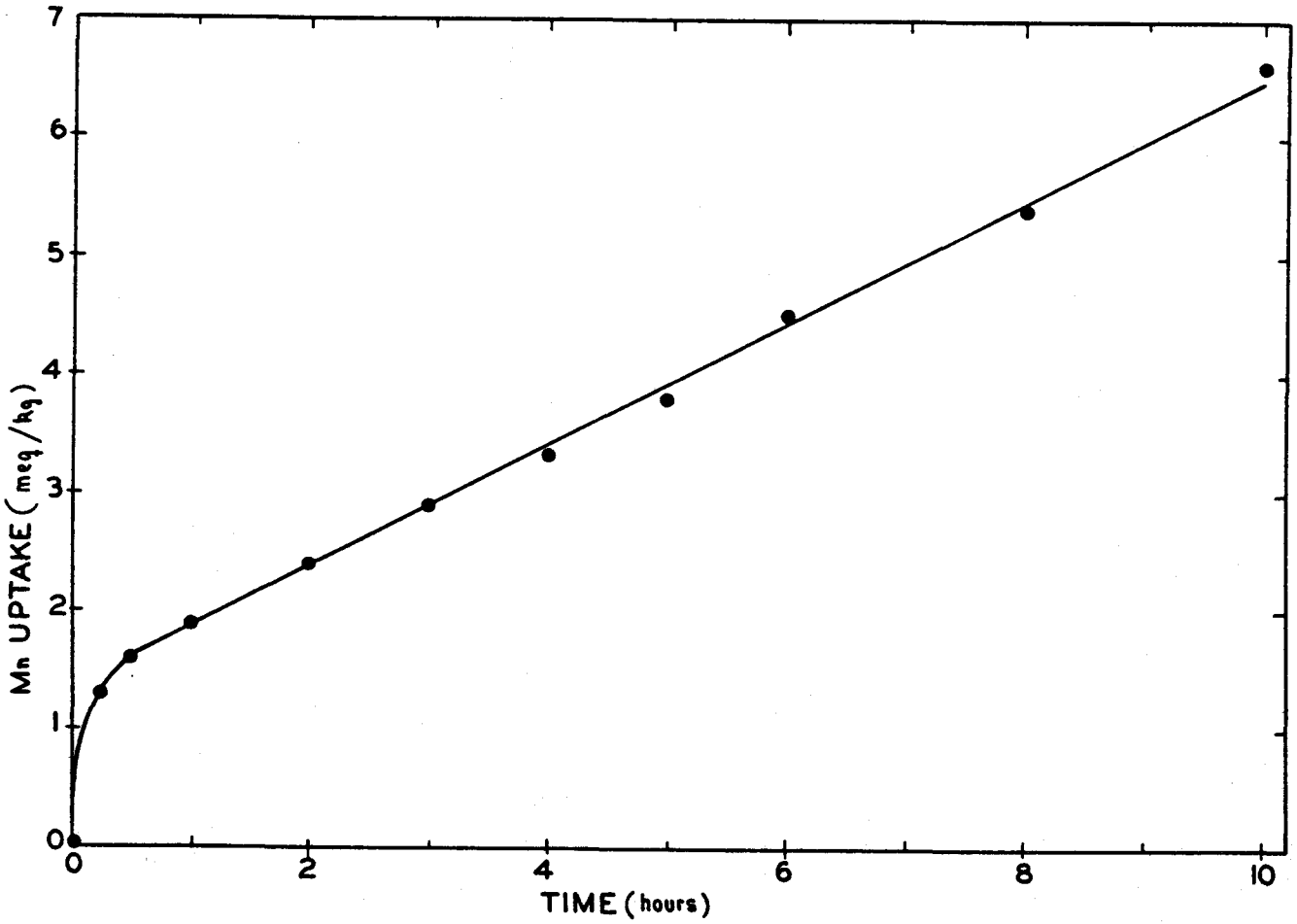

Figure 1. Uptake of Mn as a function of time from 0.05 meq $MnCl_2$ per liter at pH five. (Experiment 5-41).

course, that metabolic absorption undoubtedly did occur also during the first phase. Both the magnitude of the absorption rate (2.5 meq/kg/5 hr) during the second phase and the steady-state nature of the process suggested that a metabolic mechanism was involved. By comparison, Ca uptake, considered non-metabolic by bulk excised barley roots, was essentially nil after initial filling of the free space (Moore, Jacobson and Overstreet, 1961; cf. Moore, Mason and Maas, 1965). The reported rate of Ca uptake from 5×10^{-3} N $CaBr_2$ was only 0.1 meq/kg/5 hr.

The Role of Metabolism

To determine whether the Mn absorption was a metabolically-mediated process, the effects of several metabolic inhibitors were studied. Manganese uptake was measured in the presence of 10^{-5} M 2,4-dinitrophenol (DNP), 10^{-4} M sodium azide and 10^{-4} M sodium arsenate. In addition, Mn uptake was determined at a temperature of 0.5° C. The effects of DNP and low temperature were compared with a Mn control. To exclude the influence of Na, the effects of azide and arsenate were compared with a treatment containing 10^{-4} M NaCl.

In order to evaluate the effect of these metabolic inhibitors on both phases of uptake, absorption periods of one and six hours were used. Although the initial phase of uptake was considered complete

in 30 minutes, a one-hour period was chosen to insure the initiation of the steady-state phase. The six-hour point was selected to provide absorption sufficiently greater than the one-hour period without possible deleterious effects of physiological degeneration. The rate of absorption, calculated from the change in content in this five-hour interval, is expressed in milliequivalents of Mn absorbed per kilogram of fresh roots per five hours (meq/kg/5 hr).

The effects of the inhibitors and low temperature on the uptake of Mn are shown in Table 1. These data were taken from experiments described in Appendix Tables 2 and 3. Except at 0.5° C, little or no effect was manifested during the first hour. This would indicate that the uptake of Mn was essentially independent of metabolism during this initial phase. On the other hand, the uptake during the six-hour period and, consequently, the rate of Mn absorption was markedly reduced by all inhibitors. In fact, in the presence of DNP and at 0.5° C, there was no additional uptake after the first hour. These results certainly indicate that the uptake of Mn involved both a non-metabolic and a metabolic component. There can be little doubt that the steady-state Mn absorption was dependent on concomitant metabolism.

The uptake of Na from the chloride, arsenate and azide treatments was also determined (see Appendix Table 3). Values for the rates of absorption were 7.8, 0.7 and -0.3 meq/kg/5 hr,

respectively.[3] These rates clearly establish the effectiveness of the inhibitors at the concentrations used.

Table 1. The effects of low temperature and various metabolic inhibitors on Mn uptake from 0.05 meq $MnCl_2$ per liter at pH five. (Experiments 6-104 and 6-202).

Treatment	Uptake		Absorption Rate
	1 hr.	6 hr.	
	meq/kg		meq/kg/5 hr
Control	2.0	4.6	2.6
DNP (10^{-5} M)	1.9	1.9	0.0
0.5° C	1.5	1.5	0.0
NaCl (10^{-4} M)	1.6	3.4	1.8
Na_2HAsO_4 (10^{-4} M)	1.5	2.5	1.0
NaN_3 (10^{-4} M)	1.6	2.0	0.4

The results obtained with the metabolic inhibitors supported the choice of using one- and six-hour uptake periods. That is, the data indicate that the Mn uptake during the first hour included a sizeable non-metabolic component. Furthermore, the DNP and low temperature data showed that all subsequent Mn absorption was metabolically mediated. Therefore, by subtracting the uptake in the first hour which included the non-metabolic component from the

[3] Negative values represent, here and elsewhere in the thesis, a net loss of the ion from the root during the period involved.

total six-hour uptake, a reliable measure of the metabolic absorption rate of Mn can be obtained. Hence, any variable can be evaluated for its effect on Mn absorption independent of mass physical movement into the free space of the root. To obtain this kind of information, Mn uptake was determined in all subsequent experiments at one and six hours and the absorption rate for the five-hour interval was calculated. All results are presented in terms of this metabolic absorption rate. Although the design of the experiments did not allow a statistical analysis of the results, experience indicated that differences of $\pm$ 0.2 meq Mn/kg/5 hr were significant. Nevertheless, comparisons between individual observations were made only within experiments and conclusions were based on trends rather than absolute values.

It seems relevant at this point to define the terms "uptake" and "absorption" as they are used throughout the thesis. "Uptake" refers to the total net movement of ions into the root tissue regardless of the mechanism. It is simply a measure of the change in content during a given period. "Uptake" is used, therefore, when the metabolic and non-metabolic components are not differentiable or when the sum of the two components are involved. "Absorption" is restricted to the active or metabolic transport into plant cells, i.e. that absorption occurring during the steady-state portion of the curve (Figure 1). When used with bulk excised root studies,

"absorption" refers only to the net metabolically-mediated intake of ions. This is so because no measure of the metabolic transport of ions into the xylem (which in excised roots, are free to return to the external solution) is possible. Whenever reference is made to the passive or non-metabolic entry of ions into the root, the expression, "non-metabolic uptake" will be used.

The Effect of pH

Recognizing the influence of pH on the uptake of many monovalent and divalent ions (Hoagland and Broyer, 1940; Fawzy, Overstreet and Jacobson, 1954; Nielsen and Overstreet, 1955; Jacobson, et al., 1957; Moore, Jacobson and Overstreet, 1961; Moore, Overstreet and Jacobson, 1961), an experiment was conducted to study its effect on Mn (see Appendix Table 4). Absorption was determined at pH values of three, four, five, six and seven. However, it was found in this and other experiments that Mn was rapidly oxidized at pH values of seven or greater. Actual precipitation of Mn at pH seven and above was observed. As shown in Figure 2, this resulted in a sharp reduction in the rate of Mn absorption at pH seven. Consequently, the direct influence of pH on Mn absorption could only be evaluated at pH values of six or less. In the physiologically-favorable pH range, the rate of Mn absorption

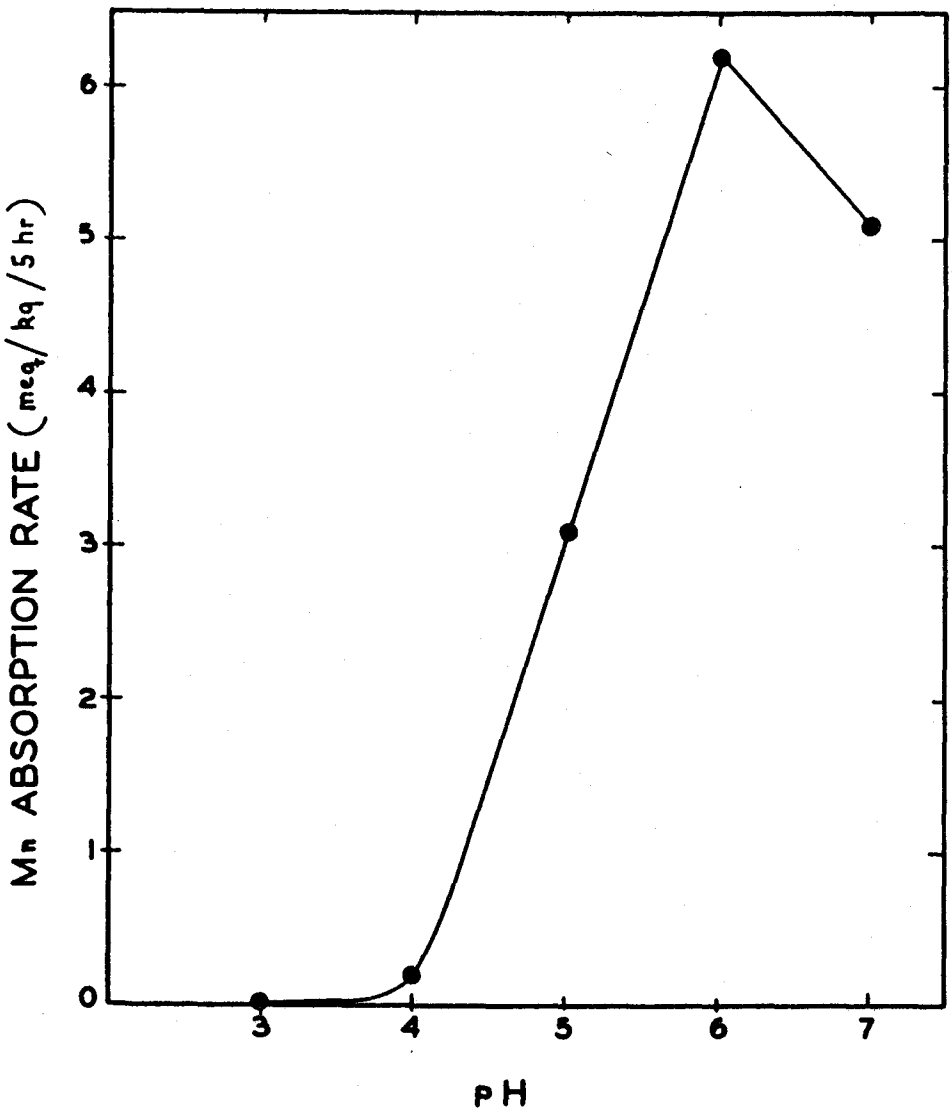

Figure 2. The effect of pH on the absorption of Mn from 0.05 meq $MnCl_2$ per liter. (Experiment 5-311).

increased rapidly with decreasing H^+ concentration. This relationship is very similar to that found for the metabolically absorbed alkali metals and Mg (Moore, Overstreet and Jacobson, 1961; Jacobson, Moore and Hannapel, 1960).

The Effect of Ambient Concentration

To further compare the absorption characteristics of Mn with those reported for Mg and the alkali cations, the rate of absorption was determined as a function of the external concentration of Mn (see Appendix Table 5). Figure 3 presents the results of Mn absorption from $MnCl_2$ solutions varying from 10^{-6} to 10^{-2} N. It can be seen that the relation between the concentration of Mn and the rate of Mn absorption was not unlike other ions (cf. Kahn and Hanson, 1957; Tromp, 1962). The absorption rate increased rapidly with initial increases in concentration up to 1.0 meq per liter. Above 1.0 meq per liter the rate approached a maximum and became essentially independent of the ambient concentration above 5.0 meq per liter. These results suggest a saturation of the transport mechanism at about 3.0 meq per liter.

In view of the injurious effects of Mn, reported by Williams and Vlamis (1957), this factor might be suspected for the change in slope in Figure 3. However, Jacobson, et al. (1961a) reported that 1.0 meq Mn per liter stimulated the uptake of K in short-term

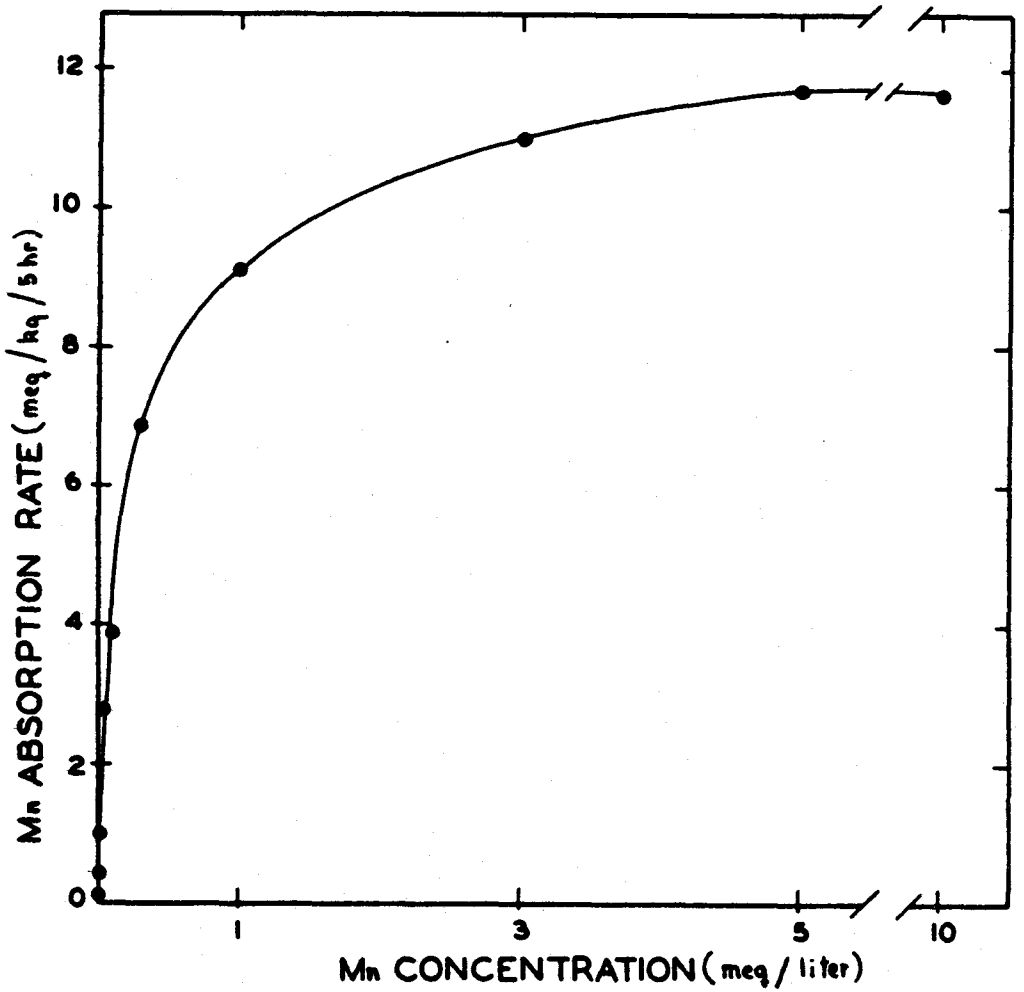

Figure 3. Absorption of Mn as a function of increasing concentrations of $MnCl_2$ at pH five. (Experiment 6-201).

experiments. This certainly is not indicative of any detrimental effect of Mn. Nevertheless, an experiment was conducted to determine if Mn toxicity were responsible for the reduction in Mn absorption. This was done by evaluating the effect of increasing concentrations of Mn on the active accumulation of K. Potassium absorption was used because it is a reliable indicator of the status of the metabolic absorption mechanism. Potassium is very rapidly absorbed by excised roots and its absorption is highly sensitive to low temperature, anoxia and many other metabolic inhibitors or toxic substances (Broyer, 1951; Ordin and Jacobson, 1955). It was expected, therefore, that impairment of the absorption mechanism by toxic levels of Mn would result in reduced absorption of both K and Mn. The experiment was designed to study K absorption from 5.0 meq KCl per liter under the influence of 0 to 25 meq Mn per liter (see Appendix Table 6).

As shown in Table 2, concentrations of less than 1.0 meq Mn per liter enhanced the absorption of K. Results of many experiments in this laboratory indicate that differences between treatments of $\pm$ 1.0 meq K/kg/5 hr are significant. This stimulatory effect of Mn thus supports the finding of Jacobson, et al. (1961a). Only at concentrations greater than 1.0 meq per liter was Mn detrimental to K absorption. However, the reduction in the rate of K absorption was not sufficient to warrant concern over physiological deterioration in

these short-term experiments except at the highest concentrations. Even then, it is not clear whether the reduction of K absorption at the higher Mn concentration was due to possible toxic effects or to competition. The increasing rate of Mn absorption with increasing concentrations to 25 meq per liter would tend to support the conclusion that the absorption mechanism was not greatly impaired. It might be noted here that in another experiment (see Appendix Table 12), even 5.0 meq Mn per liter had no significant effect on K absorption.

Table 2. The effect of increasing Mn concentration on the absorption of K at pH five. Potassium was present at 5.0 meq per liter. (Experiment 4-210).

Mn Concentration	Absorption Rate	
	K	Mn
meq/l	meq/kg/5 hr	
0.0	33.6	0.0
0.1	35.8	1.2
0.5	37.3	3.3
1.0	33.6	4.9
5.0	26.3	8.7
10.0	19.8	10.3
25.0	14.1	11.9

Further information concerning the possible injurious effects of high Mn levels was obtained by measuring the respiration of Mn

pretreated roots. The data are presented in Table 3. Oxygen uptake was determined for a period of two hours following the three-hour pretreatment in Mn. These results indicate that no serious effect of Mn was manifested except at 25 meq Mn per liter. On the basis of the uptake of Mn in other experiments, this would represent a content of about 20 meq Mn per kilogram. Nevertheless, all subsequent investigations of Mn absorption were done at 0.05 meq Mn per liter (approximately 1.4 ppm) with the exception of one experiment at 0.5 meq per liter.

Table 3. Effect of Mn pretreatment on the respiration of excised barley roots.

$MnCl_2$ Pretreatment		Oxygen Uptake Rate
Time	Conc.	
Hour	meq/l	ml/kg/hr
3	0.00	26.3
3	0.01	23.2
3	0.05	21.6
3	0.5	25.3
3	5.0	21.2
3	25.0	11.4

Influence of Other Cations

Effects of Magnesium and Calcium

On the basis of the similarity between Mn and Mg uptake, the question arose whether these two divalent ions were mutually competitive. In separate experiments, the effects of increasing concentrations of one ion on the absorption of the other were evaluated. Magnesium absorption was measured from 5.0 meq per liter $MgCl_2$ solutions with varying concentrations of Mn from 0 to 5.0 meq per liter. Absorption of Mn was determined from 0.05 meq per liter $MnCl_2$ solutions under the influence of 0 to 0.1 meq Mg per liter.

The results of these experiments are taken from a portion of Appendix Tables 7 and 8 and are summarized in Tables 4 and 5. It is apparent that Mn and Mg had a mutually depressing effect on the metabolic absorption of each other. At equivalent concentrations of Mg and Mn (5.0 meq/l), the absorption rate of Mg was reduced to only eight percent of its rate from the single-salt solution (Table 4). Conversely, the rate of Mn absorption from the mixed system (4.7 meq/kg/5 hr) was less than half that which occurred from the 5.0 meq per liter $MnCl_2$ solution shown in Figure 3. This was also true when comparing the rate of Mn absorption from 0.05 meq $MnCl_2$ per liter (Table 5). Whereas the rate of Mn absorption from

the single-salt solution was 3.6 meq/kg/5 hr, in the presence of an equivalent amount of Mg, the rate dropped to 1.7 meq/kg/5 hr. Even concentrations of the interfering ion only one-tenth that of the ion studied substantially depressed the absorption rate. In regard to the absorption rates of these two ions from mixed-salt solutions, it is noted that at equal concentrations, Mn absorption considerably exceeded that of Mg.

Table 4. The effects of increasing Mn concentration on the absorption of Mg at pH five. Magnesium was present at 5.0 meq per liter. (Experiment 5-22).

Mn Concentration	Absorption Rate	
	Mg	Mn
meq/l	meq/kg/5 hr	
0.000	14.5	0.0
0.001	14.8	0.0
0.01	14.3	0.2
0.05	13.4	0.5
0.1	11.7	0.7
0.5	4.4	1.8
1.0	2.5	2.6
5.0	1.1	4.7

Table 5. The effects of increasing Mg concentration on the absorption of Mn at pH five. Manganese was present at 0.05 meq per liter. (Experiment 5-34).

Mg Concentration	Absorption Rate	
	Mn	Mg
meq/l	meq/kg/5 hr	
0.000	3.6	-0.4
0.001	3.7	-0.2
0.005	2.6	0.0
0.010	2.7	0.0
0.025	2.0	0.2
0.05	1.7	0.4
0.10	1.5	0.7

It is especially interesting at this point to note the striking similarity between the effects of Ca and Mn on the absorption of Mg by excised barley roots (cf. Moore, Overstreet and Jacobson, 1961). These two ions appear equally effective in inhibiting Mg absorption. Parallel effects are also found in the response of Mg to pretreatments of Ca and Mn. A 30-minute exposure of the excised root material to 5.0 meq $CaBr_2$ per liter had no effect on the subsequent absorption of Mg (Moore, Overstreet and Jacobson, 1961). Likewise, pretreatment in various concentrations of $MnCl_2$ (0.01 to 10.0 meq/l) failed to have any appreciable effect on the Mg absorption rate (see Appendix Table 9).

The mutual suppression of Mn and Mg absorption cannot be explained on the basis of competition for the same transport site or carrier, however. In Tables 4 and 5, it can be seen that the sum of the absorption rates of the two ions (Mn + Mg) decreases with increasing ionic concentration of the solution. For example, in Table 4 the combined absorption rate of Mg and Mn was only 5.1 meq/kg/5 hr from a solution containing 6.0 meq of divalent cations per liter (5.0 meq Mg + 1.0 meq Mn). This rate is considerably less than the 14.5 meq of Mg absorbed in five hours from the 5.0 meq per liter $MgCl_2$ solution. In general, a similar reduction in the combined absorption rates of Mn and Mg occurred as the total cation concentration was increased in Table 5. This would not be the case if true mutual competition were involved. Instead, the resulting deficit of one ion would be compensated for by the other. Hence, the sum of the two absorption rates would have remained essentially constant or even increased due to the increasing ionic concentration of the ambient solution. It should also be noted that the inhibition of Mg absorption was clearly not the result of Mn toxicity. In either of these experiments (Tables 4 and 5) was the absorption of Mn great enough to exert toxic effects. This can be seen from Table 2 where Mn at 1.0 meq per liter had no harmful effect on K absorption, yet the Mn absorption rate exceeded that in both Tables 4 and 5.

In view of the regulatory effects of Ca on ion absorption (Viets, 1944; Kahn and Hanson, 1957; Jacobson, Moore and Hannapel, 1960; Jacobson, et al., 1961a; Moore, Overstreet and Jacobson, 1961; Epstein, 1961; Waisel, 1962b; Hooymans, 1964), it seemed advisable to evaluate the effect of Ca on the absorption of Mn. Varying amounts of $CaCl_2$ were added to 5×10^{-5} N $MnCl_2$ solutions to obtain treatments containing 0 to 10.0 meq Ca per liter. The data, summarized in Table 6, were taken from a part of the experiment described in Appendix Table 10. An appreciable stimulation of Mn absorption resulted from the presence of Ca at concentrations up to 0.5 meq per liter, a ratio of Ca to Mn concentrations of 10:1. Increases in Ca concentrations above this level, however, exerted a depressing effect.

Stimulation of ion absorption by Ca, first reported by Viets (1944), has received several explanations from various investigators. Its influence has been ascribed to a modification of the selective permeability of the cell membrane (Jacobson, et al., 1961a; Jacobson, Moore and Hannapel, 1960; Moore, Overstreet and Jacobson, 1961; Waisel, 1962b), an increase in the affinity between the carrier and ion (Kahn and Hanson, 1957; Tanada, 1962), and its essentiality in maintaining the integrity of the selective ion transport mechanism (Epstein, 1961). Whether the enhanced absorption of Mn by Ca was the result of any particular one of these factors cannot be

stated with certainty. Nevertheless, Ca-stimulation of Mn absorption, in all probability, was the result of the same kind of mechanism which was involved in the stimulation of some monovalent ions. Reduction of the absorption rate by increased levels of Ca may simply reflect the overwhelming concentration of Ca with respect to Mn (Ca:Mn ratios 20:1 or greater). At any rate, competition between Ca and Mn for the Mn-carrier does not appear likely. This is obvious both from the stimulation of Mn absorption by Ca and from the nearly complete lack of Ca absorption by this tissue shown in Table 6 (cf. Moore, Jacobson and Overstreet, 1961). Even at a Ca concentration of 10.0 meq per liter, only 0.2 meq of Ca was absorbed in five hours.

Table 6. The effects of increasing Ca concentration on the absorption of Mn at pH five. Manganese was present at 0.05 meq per liter. (Experiment 5-35).

Ca Concentration	Absorption Rate	
	Mn	Ca
meq/l	meq/kg/5 hr	
0.00	2.9	-0.2
0.01	3.1	-0.1
0.05	3.5	0.0
0.1	3.7	0.2
0.5	3.3	0.1
1.0	2.6	0.1
5.0	1.3	0.2
10.0	0.9	0.2

The outstanding feature of these data is the completely opposing effects of Ca on the absorption of Mn, found in this study, and on the absorption of Mg reported by Moore, Overstreet and Jacobson (1961). Whereas 0.5 meq Ca per liter stimulated Mn absorption, it reduced the uptake of Mg by about 80%. This distinction adds additional support to the supposition that Mn and Mg, two metabolically-absorbed divalent ions, are transported via different sites.

Since Ca markedly inhibited the absorption of Mg and slightly stimulated that of Mn, the question immediately arose whether Ca would overcome the Mg effect on Mn. In other words, would Ca, by blocking Mg absorption, eliminate the Mg interference of Mn absorption? Several parallel relationships exist where Ca exerts this very effect. For instance, it has been shown that, by inhibiting the absorption of Li, Ca completely eliminated the Li interference on K absorption (Jacobson, Moore and Hannapel, 1960). Calcium has also been found to prevent competition between K and Na (Jacobson, et al., 1961a; Epstein, 1961) and between K and Mg (Moore, 1960). In both cases, K absorption was enhanced while the absorption of Na and Mg was reduced or abolished.

In order to thoroughly study the Ca-Mn-Mg relationship, several experiments were conducted. It was shown above (Tables 5 and 6) that the individual effects of Ca and Mg on Mn absorption were

a function of their concentration in the ambient solution. Consequently, it seemed pertinent to study increasing concentrations of one ion (Ca or Mg) in the absence and presence of the other. In the first experiment (see Appendix Table 8), Mg concentrations from 0 to 0.1 meq per liter were imposed on 5×10^{-5} N $MnCl_2$ solutions. Absorption was then compared with duplicate treatments containing, in addition, 0.05 meq Ca per liter. Figure 4 depicts the results of this experiment. As pointed out above in the discussion of Table 5, Mg is highly effective in reducing the absorption of Mn. The presence of only 0.005 meq Mg per liter markedly reduced the rate of Mn absorption. Most unexpected, however, was the effect of Ca in the presence of Mg. Instead of eliminating the Mg interference of Mn absorption, the presence of Ca led to further inhibition. This was true at all Mg levels studied. As shown previously, Ca alone had a slight stimulatory effect on Mn absorption. However, it is obvious that an exceedingly small amount of Mg was capable of reversing this effect of Ca. As little as 0.001 meq of Mg per liter converted an eight percent Ca stimulation into an eight percent reduction.

Notably similar results were obtained from another experiment in which the concentration of Mn and Ca were both ten-fold higher (Figure 5, see Appendix Table 11). As before, suppression of the Mn absorption rate by additional increments of Mg was more

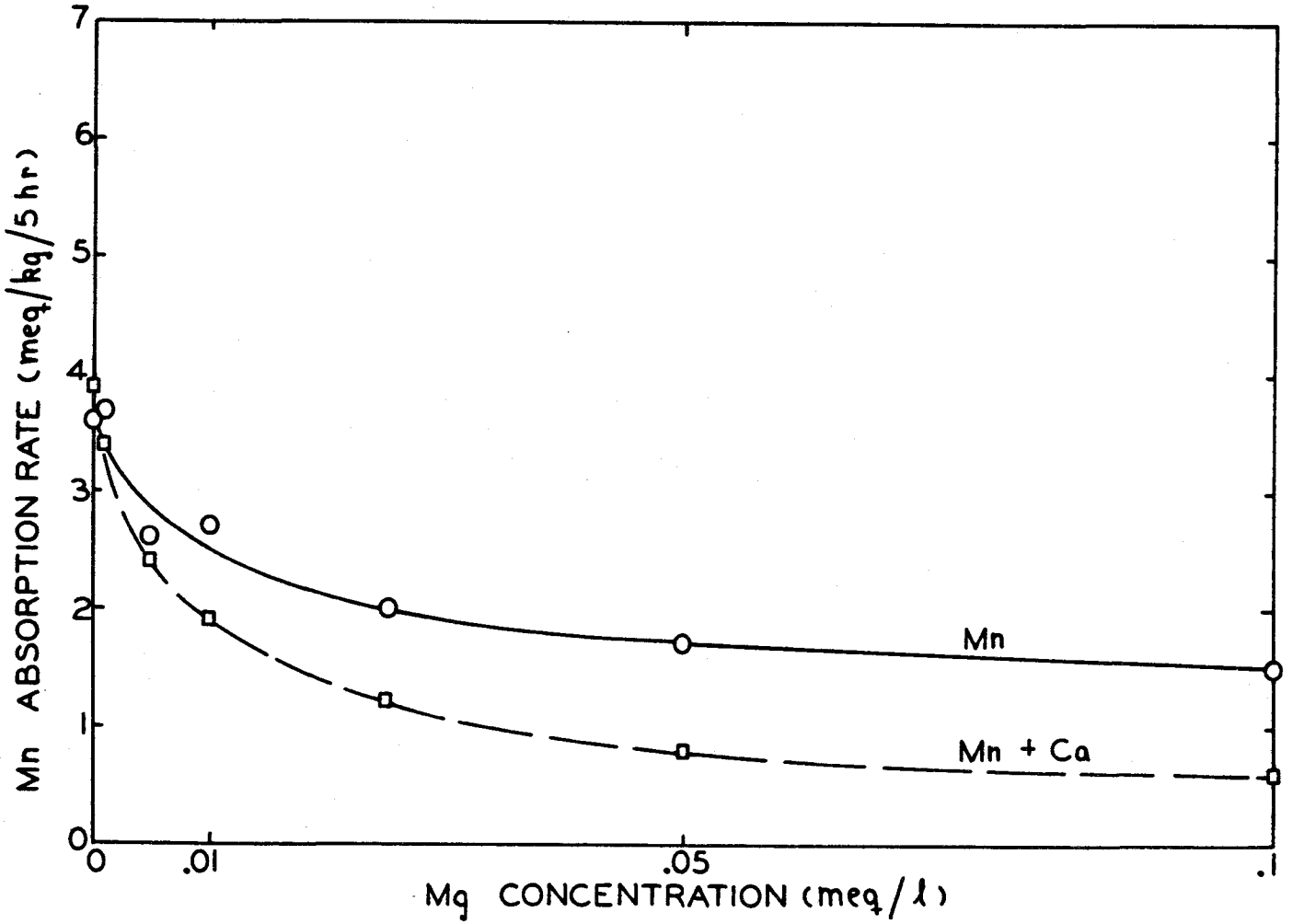

Figure 4. The effects of increasing Mg concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 meq per liter. (Experiment 5-34).

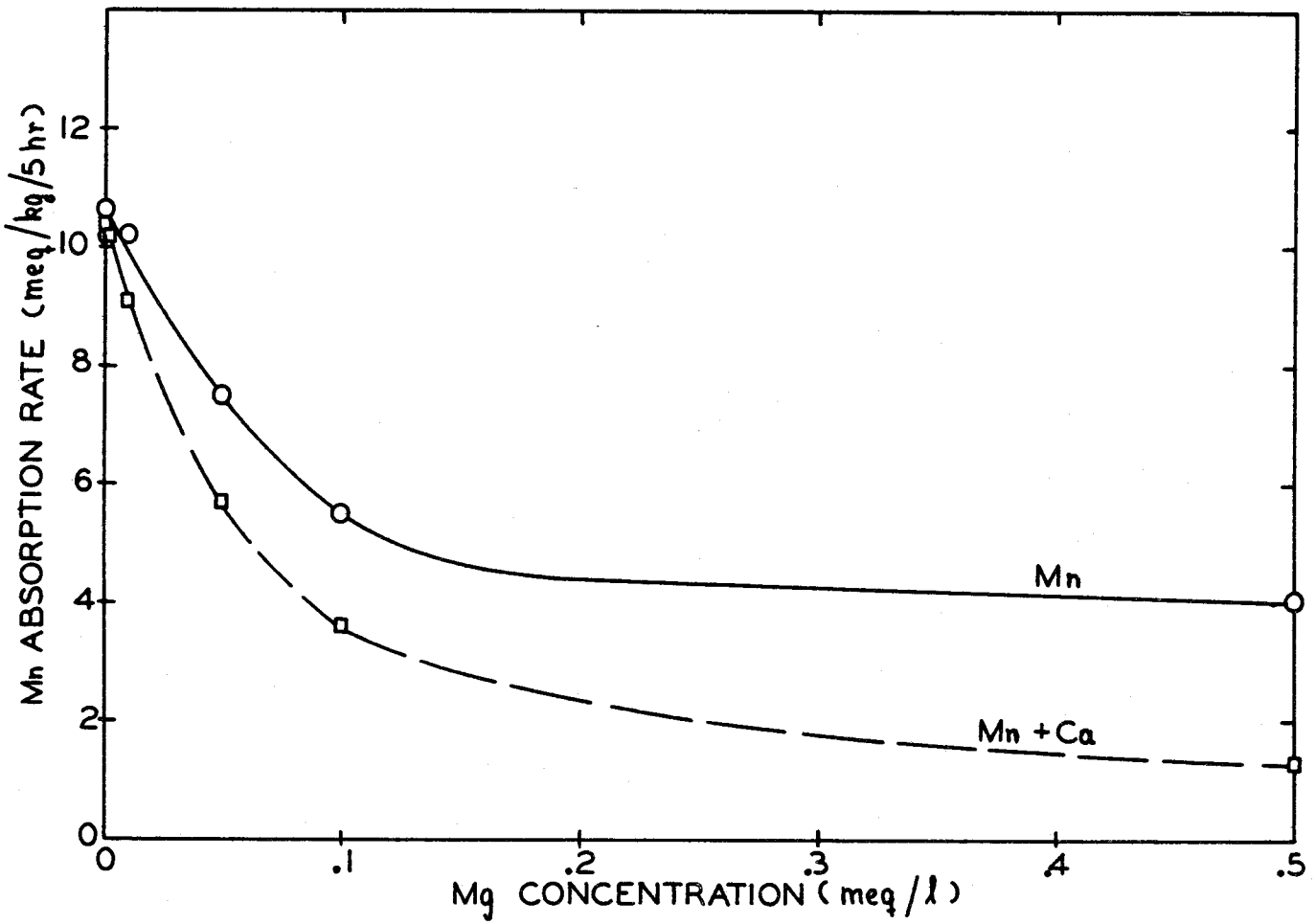

Figure 5. The effects of increasing Mg concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.5 meq per liter. (Experiment 5-33).

pronounced in the presence than in the absence of Ca.

It is especially noteworthy in these experiments that the total cation absorption from a Ca-Mg-Mn solution was extremely low (Tables 7 and 8). Although Ca absorption by bulk excised roots is known to be negligible, both Mn and Mg were rapidly absorbed from single-salt solutions. The rate of Mn absorption from 0.5 meq $MnCl_2$ per liter was 10.3 meq/kg/5 hr (Figure 5). Magnesium absorption from 5.0 meq $MgCl_2$ per liter occurred at the rate of 14.5 meq/kg/5 hr (Table 4). However, as can be seen in Tables 7 and 8, when all three ions were combined at equivalent concentrations, cation absorption was almost totally inhibited. Calcium absorption remained nil and the sum of the Mg and Mn absorption rates from 0.05 and 0.5 meq per liter solutions was only 1.6 and 2.9 meq/kg/5 hr, respectively (Tables 7 and 8). It is difficult to see how this data can be explained on the basis of competition. The influence of these ions on the absorption of each other obviously was exerted at some point other than the transport site. As a result, the efficiency of the absorption mechanism became severely restricted. To obtain a measure of the impairment of the entire transport mechanism, the effect of Ca, Mg and Mn on the absorption of K was evaluated. As pointed out previously, K absorption provides a reliable indicator of the absorbing capacity of the root tissue. The experiment included both individual treatments of Ca, Mg and

Mn and various combinations of these ions (see Appendix Table 12).

Table 7. Absorption rates of Mn, Ca and Mg as influenced by increasing concentrations of Mg at pH five. Manganese and Ca were present at 0.05 meq per liter. (Experiment 5-34).

Mg Concentration	Absorption Rate		
	Mn	Ca	Mg
meq/l	meq/kg/5 hr		
0.000	3.9	0.2	-0.1
0.001	3.4	0.4	-0.1
0.005	2.4	-0.1	-0.1
0.010	1.9	0.1	0.1
0.025	1.2	0.1	0.7
0.05	0.8	0.0	0.8
0.1	0.6	0.0	0.8

Table 8. Absorption rates of Mn, Ca and Mg as influenced by increasing concentrations of Mg at pH five. Manganese and Ca were present at 0.5 meq per liter. (Experiment 5-33).

Mg Concentration	Absorption Rate		
	Mn	Ca	Mg
meq/l	meq/kg/5 hr		
0.000	10.5	0.0	-0.2
0.001	10.3	0.1	-0.1
0.01	9.1	0.1	0.1
0.05	5.7	0.1	0.7
0.1	3.6	0.1	1.1
0.5	1.3	-0.1	1.6

Data for the absorption rates of these ions are presented in Table 9. It is immediately apparent from these results that although the absorption of Mn and Mg again was severely inhibited in the Ca-Mg-Mn system, K absorption was greatly enhanced. Both Ca and Mg markedly increased the absorption of K while Mn at this concentration had little or no effect. In combination with Mg, the Ca effect predominated, presumably by blocking the absorption and/or binding of Mg. In the Ca-Mn treatment, Mn drastically reduced the effect of Ca, possibly because Mn was more strongly bound than Ca. As Mg and Mn are mutually antagonistic, the influence of these two ions together was apparently the net result of their individual effects. The combined effect of all three cations (Ca, Mg, Mn) was comparable to the highly stimulatory effect of Ca alone. This was remarkable in view of the negligible absorption of divalent cations from this system. It can be seen in Appendix Table 12 that this enhanced absorption of K was not due to the increased total concentration of divalent cations. No appreciable effect was gained by doubling or tripling the concentrations of Ca and Mg. As pointed out earlier (Table 2), concentrations of Mn greater than 5.0 meq per liter depressed the absorption of K.

It must be emphasized here that although the carrier mechanism was nearly incapable of transporting divalent cations from the Ca-Mg-Mn system, its capacity to transport K was certainly not

impaired. Furthermore, it should be noted that whatever the effect of the divalent cations, it must have been exerted at the extracellular surface since the absorption of these ions was extremely limited or negligible.

Table 9. The effects of Ca, Mg and Mn on the absorption of K at pH five. The concentrations of all ions were 5.0 meq per liter. (Experiment 4-28).

Treatment	Absorption Rate			
	K	Ca	Mg	Mn
	meq/kg/5 hr			
Control	20.1			
Ca	42.0	-0.1		
Mg	36.5		4.5	
Mn	20.9			9.3
Ca + Mg	42.4	-0.2	0.5	
Ca + Mn	22.3	0.0		7.8
Mg + Mn	33.2		0.2	4.1
Ca + Mg + Mn	42.8	-0.2	0.5	0.8

To follow up on the Ca-Mg-Mn interaction, another experiment was designed to study the effect of increasing concentrations of Ca in the absence and presence of Mg. Solutions of 5×10^{-5} N $MnCl_2$ were subjected to increasing Ca concentrations from 0 to 1.0 meq per liter. To a series of identical treatments, 0.05 meq Mg per liter was added. The results are presented in Figure 6 (see Appendix Table 10). The effect of Ca in the absence of Mg, noted previously in Table 6, is shown in the upper curve. At

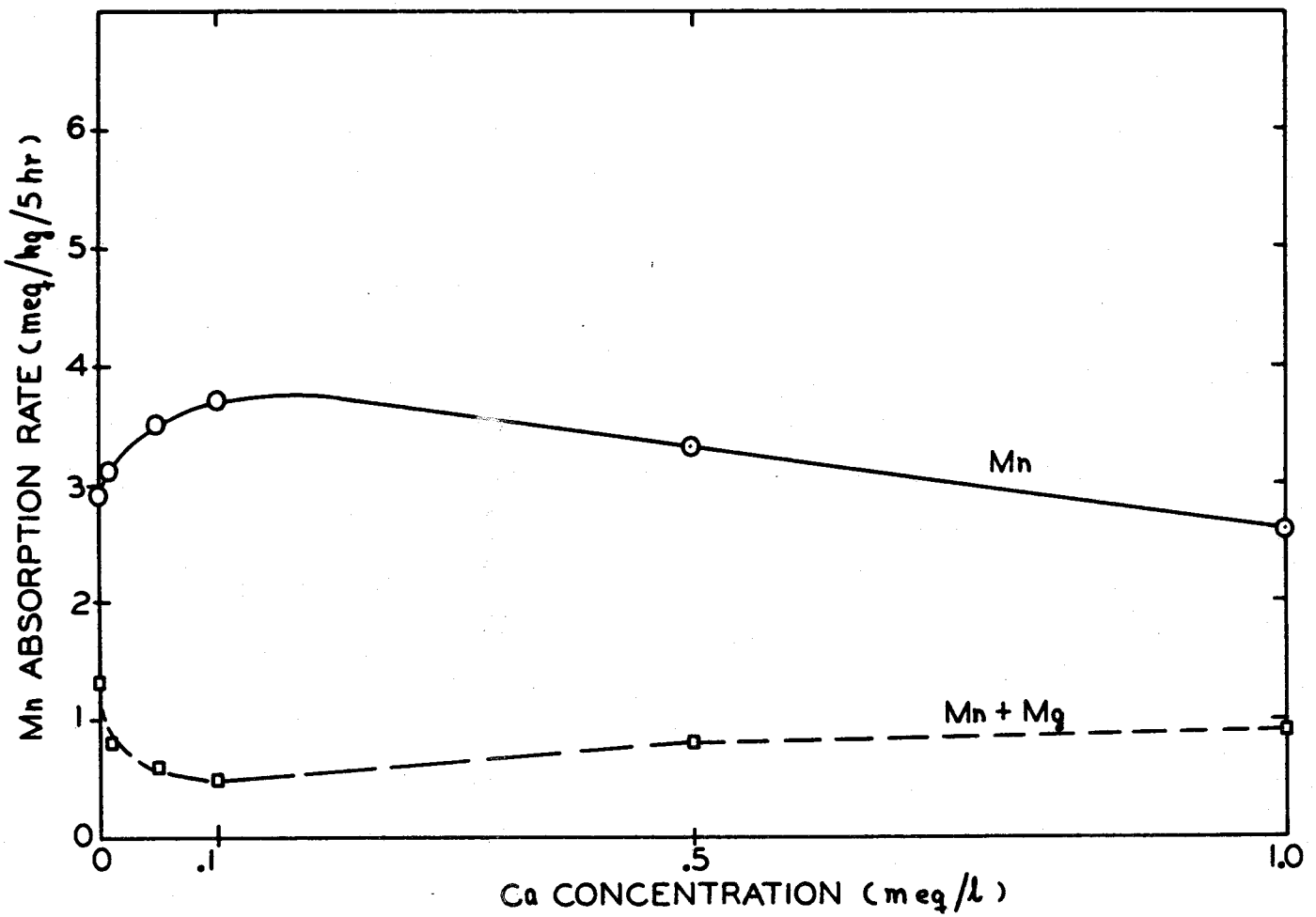

Figure 6. The effects of increasing Ca concentration on the absorption of Mn in the absence and presence of Mg at pH five. The concentrations of Mn and Mg were 0.05 meq per liter. (Experiment 5-35).

concentrations from 0.01 to 0.5 meq per liter, Ca had a stimulatory effect on Mn absorption. Above this concentration range the absorption of Mn became impeded by Ca.

Though not surprising in view of previous results, the lower curve in Figure 6 is interesting. Again the combination of very small amounts of Ca and Mg led to a reduction in Mn absorption. However, when Ca concentrations exceeded that of Mg by a factor of ten or greater, the effect began to resemble that of Ca alone. That is, it appears that the two curves might converge at greater concentrations. In fact, in Table 10 of the appendix, it can be seen that in the absence of Mg, the Mn absorption rate in the presence of 10.0 meq Ca per liter was equivalent to a mixture of 1.0 meq Ca and 0.05 meq Mg per liter.

One explanation for the effect of Ca, is that by mass action, it simply displaced Mg from its reactive site. In other words at high concentrations of Ca, relative to Mg, the former Mg-activated sites became Ca saturated. The net result would then appear to be due to Ca alone. The predominating effect of Ca was also pointed out in discussing the combined effect of Ca and Mg on K absorption in Table 9.

As previously noted, the total divalent ion absorption from the Ca-Mg-Mn solutions in this experiment (see Appendix Table 10), was extremely low considering the magnitude of absorption of Mg and Mn

from single-salt solutions.

As all of the above data were obtained at pH five, it seemed advisable to evaluate the Ca-Mg-Mn interaction at other H^+ concentrations. The importance of the hydrogen ion in studying interrelationships between ions was well demonstrated by Jacobson, Moore and Hannapel (1960). They found that the effect of Ca on the absorption of Na, K, Rb and Cs was greatly dependent upon the pH of the ambient solution. Whereas Ca stimulated the absorption of these ions at low pH values, it markedly depressed absorption above pH six. The relationship between Mg and K has likewise been shown to be a function of the H^+ concentration (Moore, 1960).

In light of these findings, an experiment was designed to study the effects of Ca and Mg individually and together on the absorption of Mn in the pH range of four to seven. The results, taken from Appendix Table 13, are illustrated in Figure 7. As expected, there was little absorption at pH four from any treatment. The rates at pH five were comparable to those of previous experiments with the exception of a lack of stimulation from Ca. At pH six, Ca likewise appeared to be without effect on Mn absorption. Magnesium, on the other hand, suppressed the increased absorption rate which resulted from decreasing H^+ concentration. The additional depression from Ca when combined with Mg was fairly constant in the physiological pH range. As stated previously, the data obtained at pH seven are

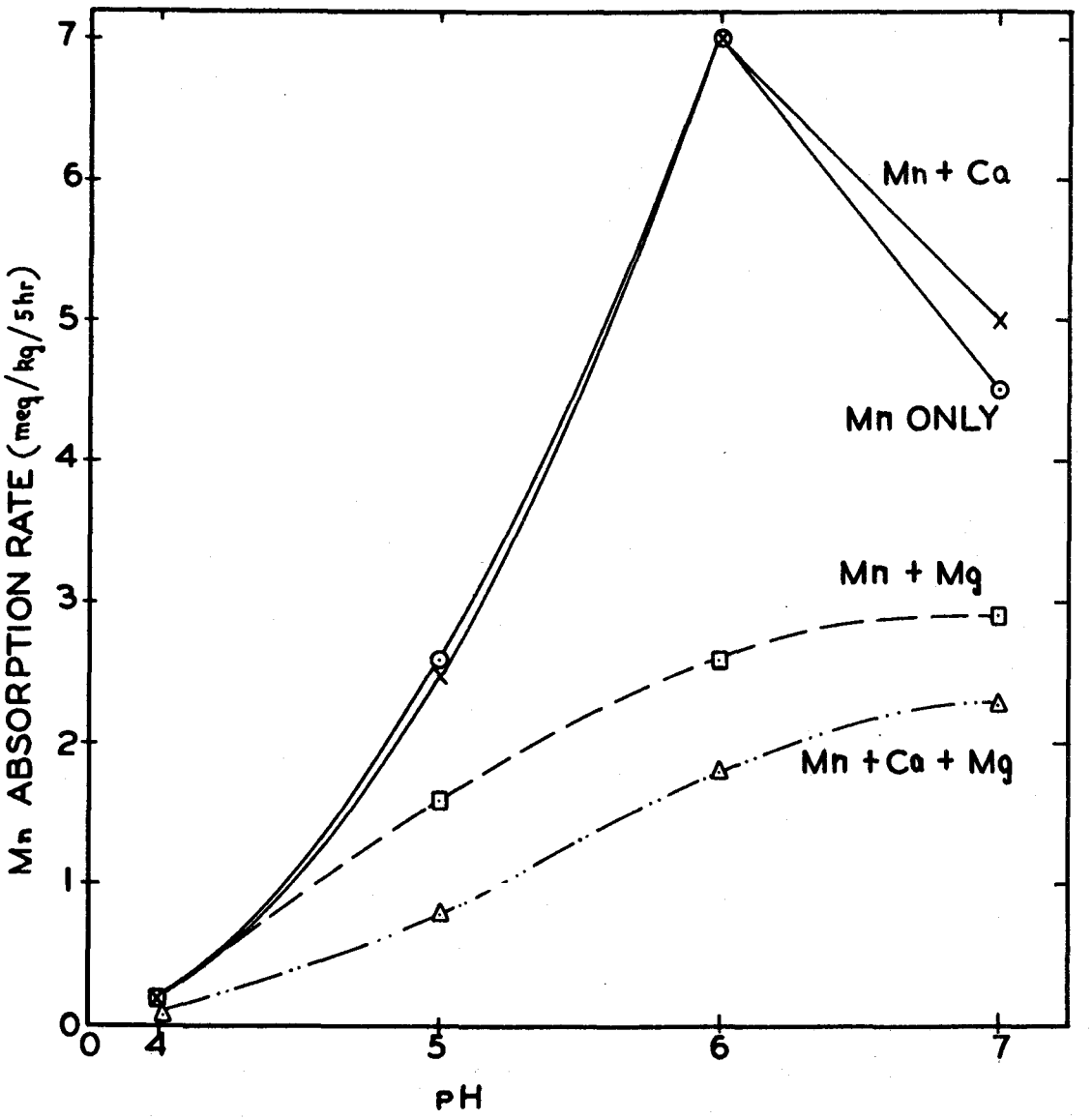

Figure 7. The effects of Ca and Mg on the absorption of Mn at various pH values. (Experiment 5-315).

open to question, due to possible precipitation of Mn in the ambient solution. Nevertheless, the relationship between the various treatments remained the same.

The lack of Ca stimulation in this experiment merits some attention at this time. The failure to obtain a stimulation from Ca may well be related to contamination of the solution by Mg. This would appear to be the most logical explanation in view of the depressing effect from exceedingly small amounts of Mg in the presence of Ca (Figure 4). The source of Mg could be either from contamination in the treatment solution or leakage from the plant tissue. Even though reagent-grade chemicals were used, Mg was a common contaminant in the Ca salts (0.003%). Although this represented a very small amount of Mg, it may well have contributed to a threshold level of Mg in the solution. In isolated instances, contamination from improperly washed glassware and other places was a possibility.

The most obvious source of Mg was the loss of exchangeable and internal Mg from the root material. As noted in the materials and methods section, the seedlings were grown in a media which contained Mg. Although the roots were well washed to remove Mg and other ions adhering to the root surfaces, additional losses of Mg usually occurred in the absorption solution. The extent of the leakage was variable and could not be controlled. A loss of Mg

equivalent to one meq per kilogram of roots would result in an ambient solution concentration of 0.001 meq Mg per liter. As noted previously in reference to Figure 4, this amount of Mg in the presence of Ca would account for the lack of a stimulation from Ca. However, it must be recognized that the Mg concentration on the abscissa of Figure 4 does not include the loss of Mg which occurred during that experiment (see Appendix Table 8). Consequently, suppression of Ca stimulation must be due to Mg losses over and above that which occurred in Experiment 5-34.

Data obtained from 26 experiments in which Mn absorption was determined in the absence and presence of 0.05 to 0.5 meq Ca per liter revealed effects of Ca ranging from a stimulation to a reduction of Mn. Those cases in which no effect or a reduction from Ca occurred are believed to be the result of a Ca-Mg interaction. As will be seen later in the thesis, a few other ions are also highly effective inhibitors of Mn absorption. However, the possibility of contamination or leakage of these ions to the extent required is extremely remote.

Effects of Other Polyvalent Cations

In view of the regulatory effects of Ca and Mg on the absorption of Mn, additional experiments were subsequently conducted to study the effects of other divalent and polyvalent ions such

as Sr^{++}, Ba^{++}, Fe^{++}, Zn^{++}, Cu^{++}, Fe^{+++}, Al^{+++} and La^{+++}. The literature contains many observations in which the effects of polyvalent cations on ion absorption are similar. Viets (1944) was the first to show that a number of divalent and trivalent cations (Ca, Mg, Sr, Ba and Al) all had a stimulatory effect on the absorption of K and Br. Two other trivalent ions, La and Ce, have also been added to the list of cations which strongly enhance K absorption (Fawzy, Overstreet and Jacobson, 1954). Jacobson, et al. (1961a) found that not only did Ca, Mg, Sr, Mn, Al and La stimulate K absorption, but with the exception of Mg, all markedly depressed the absorption of Li.

These results were interesting in that Li presented a situation where the effects of Mg were different from other polyvalent cations. That Mg affects absorption differently than other divalent cations was also shown by Epstein (1961). His results indicated that Sr, Ba, Mn and Zn, to varying degrees, were as nearly effective as Ca in reversing the inhibition of Rb absorption by Na. In contrast, Mg exerted practically no reversal effect. This was also true when Mg was compared with Ca in reversing the interference of K transport by Na.

In light of these observations, experiments were conducted to determine whether the non-specific action of polyvalent cations existed in their effects on Mn absorption. Furthermore, it was of

interest to know if the effects resembled those of Ca or Mg in the interactions described above.

Strontium and Barium. In the first experiment, the effects of the other alkaline earth cations, Sr and Ba, were compared with those of Ca and Mg. The experiment was designed to study the effects of Ca, Mg, Sr and Ba individually and in all combinations of two on Mn absorption (see Appendix Table 14). The various treatments and results are presented in Table 10.

Table 10. The effects of Ca, Mg, Sr and Ba on the absorption of Mn at pH five. The concentrations of all ions were 0.05 meq per liter, including Mn, which was present in all treatments. (Experiment 5-316).

Treatment	Mn Absorption Rate
	meq/kg/5 hr
Control	3.8
Ca	5.1
Mg	2.4
Sr	3.8
Ba	3.4
Ca + Mg	1.2
Ca + Sr	4.3
Ca + Ba	3.9
Mg + Sr	1.6
Mg + Ba	1.6
Sr + Ba	3.1

About midway through the absorption period, the temperature uncontrollably climbed to 32° C. Although this probably accounted for a slightly higher than average absorption, it was not considered a serious problem. The data of Jacobson, et al. (1957) showed that at pH five, K absorption increased only slightly with an increase in temperature from 25 to 35° C. Furthermore, they found that this was the optimum temperature range for the three-hour absorption period. A comparison of the effects of Ca, Mg and Ca + Mg in Table 10 with those in prior experiments (Figures 4 and 6) indicates that in spite of the temperature rise, the relative effects were the same.

The respective stimulation and depression by Ca and Mg do not appear to be duplicated by either Sr or Ba. Rather, these ions seem to have little or no effect on Mn at the concentrations involved. As before, the effect of Ca in the presence of Mg led to further inhibition. In this respect, both Sr and Ba could be substituted for Ca, although the depressive effect of these ions, in combination with Mg, was not as pronounced as for Ca. Conversely, it can be seen that neither Sr nor Ba duplicated the effect of Mg when present with Ca. Instead, the absorption of Mn when combinations of Ca and Sr or Ca and Ba are present, was approximately intermediate between the absorption rate when these ions were present singly.

Once again, attention should be given to the total absorption

of Mn + Mg (see Appendix Table 14). The combined absorption rate for these two ions, from the Ca-Mg-Mn system, was quite low (2.6 meq/kg/5 hr). Similarly, when either Sr or Ba was substituted for Ca, the rates were also low.

The effects of different ion pairs as compared to individual ion effects might also be evaluated. Considering Ca first, the data reveal that Mn absorption from either Sr or Ba solutions was enhanced by addition of Ca. As noted, Ca when coupled with Mg resulted in further reductions. On the other hand, Sr reduced the absorption of Mn when combined with either Ca, Mg or Ba as compared to the effect of these ions alone. The same is true for the effect of the various combinations with Ba. That is, absorption rates in the presence of either Ca, Mg or Sr alone were substantially reduced with the addition of Ba.

The slight depressing effect of Ba was of interest as was the ability of Ca to block it. Consequently, an experiment was set up to determine if the Ba effect was concentration dependent and to observe the protective effect of Ca (see Appendix Table 15). The concentration of Ba was varied from 0 to 1.0 meq per liter, Ca was added to obtain 0.5 meq per liter and the Mn concentration was 0.05 meq per liter, as usual. The results, illustrated in Figure 8, showed a gradual decline in the Mn absorption rate with increasing concentrations of Ba. Although the suppressive effect of Ba was

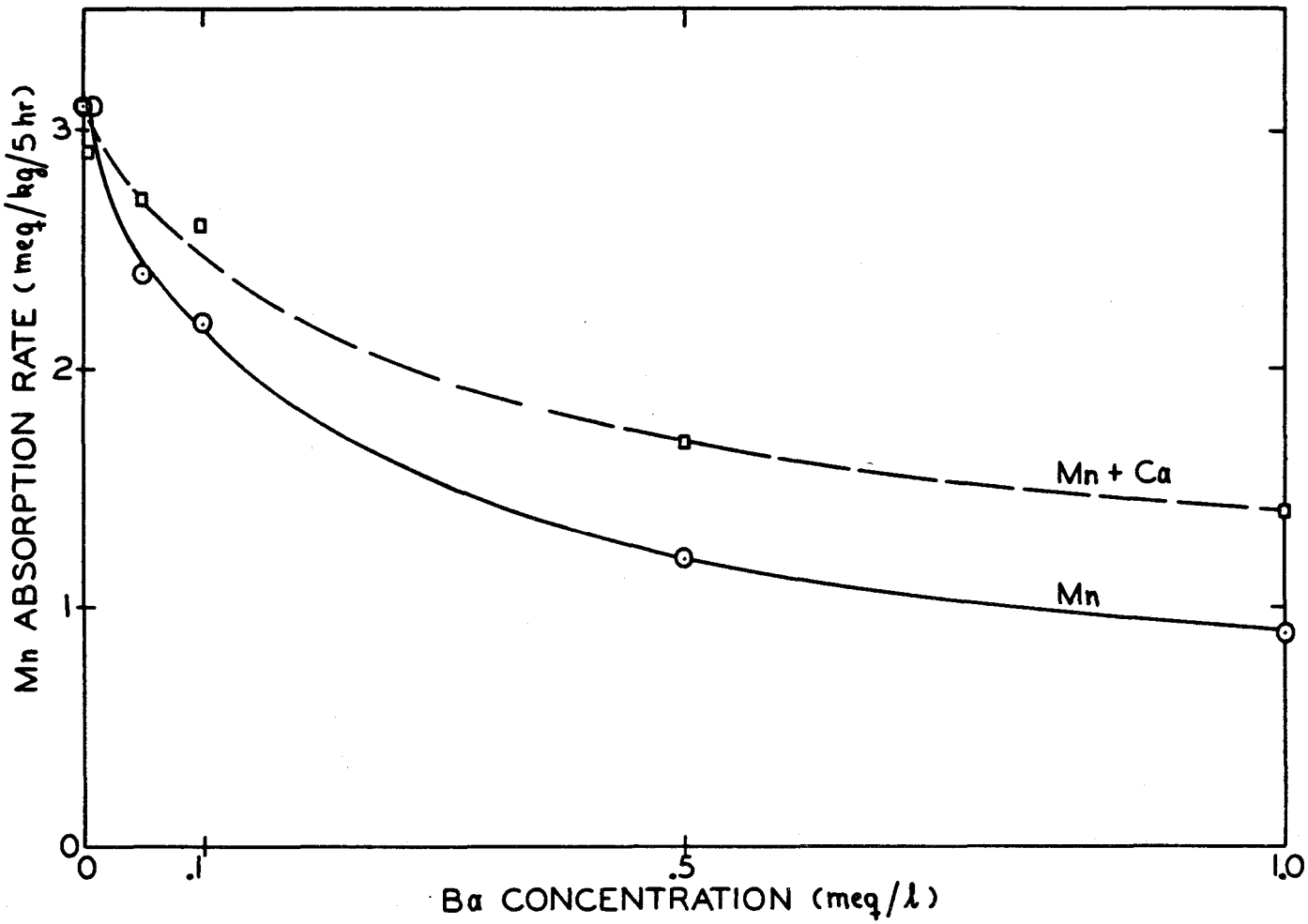

Figure 8. The effects of increasing Ba concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-312).

quite pronounced at 1.0 meq per liter (a Ba:Mn ratio of 20:1), it is obvious that Ba is much less effective than Mg. Whereas 0.005 meq Mg per liter reduced the absorption of Mn by nearly 30% (Table 5), this amount of Ba had no effect. Furthermore, unlike the Ca-Mg treatment where Ca enhanced the effect of Mg, the effect of Ba was decreased by Ca. It appears, therefore, that the effect of Ba was intermediate between that of Ca and of Mg. Of course, since Ba did not exhibit any stimulatory effects, the depressive effect would be expected at lower concentrations than for Ca. In the mixed Ba-Ca system, the net effect on Mn absorption was probably the result of the stimulatory or protective effect of Ca and the depression due to Ba.

Ferrous Iron. The next divalent cation that was considered was that of ferrous iron. Manganese absorption was studied under increasing concentrations of ferrous chloride from 0 to 0.1 meq per liter in the absence and presence of Ca and of Mg. Manganese, Ca and Mg were each employed at a concentration of 0.05 meq per liter. The results of this experiment, described in Appendix Table 16, are plotted in Figure 9. A comparison of these curves with those in Figure 4 reveals an immediate similarity between the effects of Mg and Fe^{++}. Ferrous iron, like Mg, depressed the absorption of Mn at extremely low concentrations. Also, Fe^{++} was capable of reversing the stimulatory effect of Ca. This response

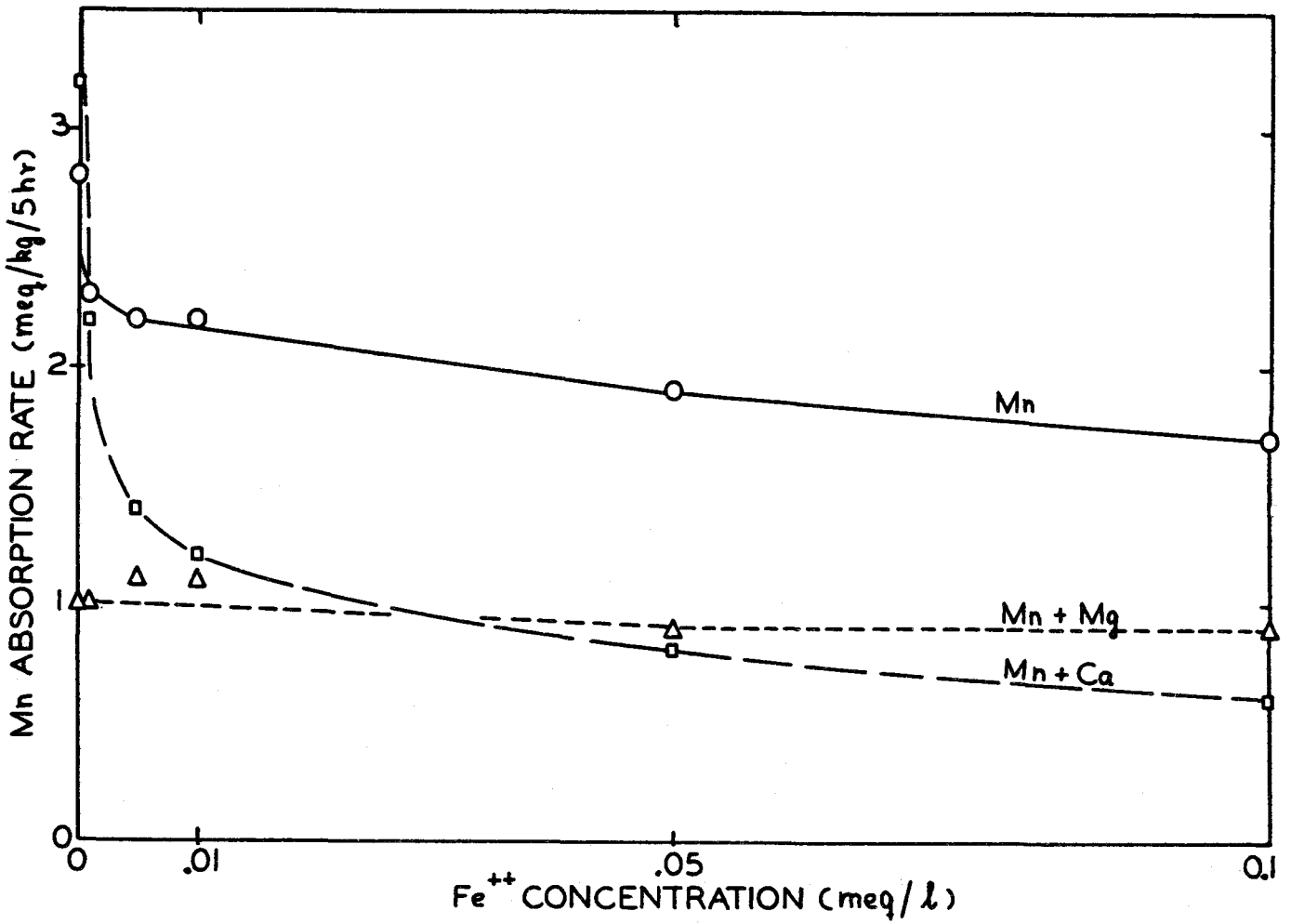

Figure 9. The effects of increasing Fe^{++} concentration on the absorption of Mn in the absence and presence of Ca and of Mg at pH five. The concentrations of Mn, Ca and Mg were 0.05 meq per liter. (Experiment 5-318).

was manifested at only 0.001 meq Fe^{++} per liter, a concentration only one-fiftieth that of Mn. As in the case of Mg, the suppression of Mn absorption by Fe^{++} was accentuated by the addition of Ca. No appreciable effect from Fe^{++} was apparent in the presence of Mg, however. Apparently 0.05 meq Mg per liter completely eliminated that portion of Mn absorption which was affected by Fe^{++}. It should be noted that the effect of 0.05 meq Mg per liter was considerably greater than an equivalent concentration of Fe^{++}.

Another interesting feature of this experiment was the high accumulation of iron. Figure 10 depicts the absorption of Fe as a function of concentration. It must be kept in mind that this large uptake occurred in the presence of 0.05 meq Mn per liter. This is surprising in view of the commonly recognized antagonism between Fe and Mn (Jackson, In press). Competitive inhibition of Fe absorption by Mn has been found recently in excised rice roots (Shim and Vose, 1965). Comparing rates, the absorption of Fe was considerably higher than that of Mn. At equal concentrations (0.05 meq/l), the absorption of Fe was nearly three times that of Mn. Absorption of Mn from a single-salt solution was only half that of Fe from the mixed system. The addition of 0.05 meq of Ca had little effect on the absorption of Fe, whereas Mg caused a definite reduction at the higher Fe^{++} concentrations. Whether this absorption is completely metabolically mediated is not known. According to Shim

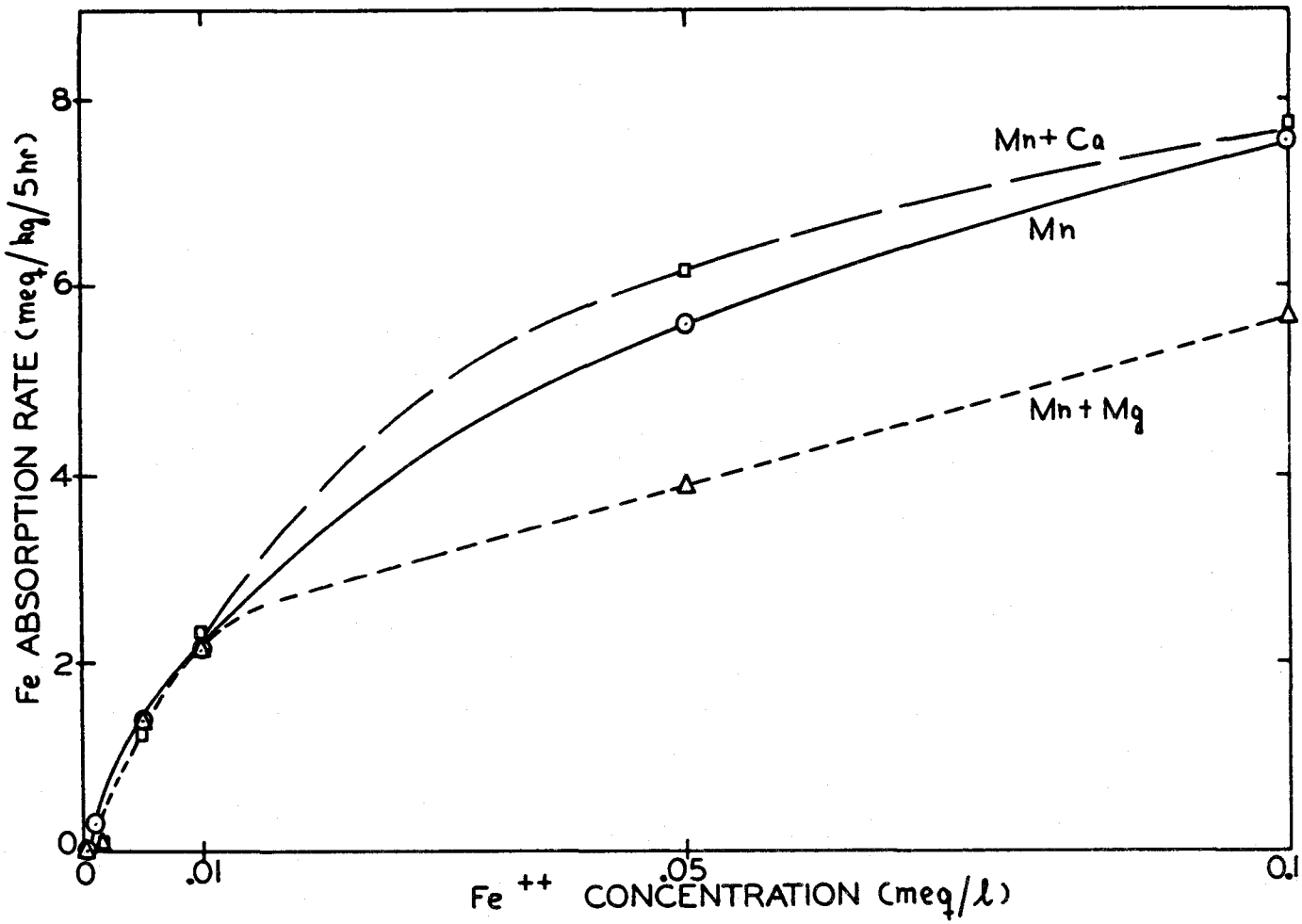

Figure 10. Absorption of Fe as a function of increasing concentrations of $FeCl_2$ in the presence of Mn, Mn + Ca and Mn + Mg at pH five. (Experiment 5-318).

and Vose (1965), iron absorption by excised rice roots is characteristic of an active process. However, their experiments were conducted with solutions of $FeCl_3$ rather than $FeCl_2$.

The results reported here certainly point out the importance of further study of the interrelationships between the heavy metals and their absorption at the cellular level.

Zinc. The results of a comparable experiment in which Zn-Mn relationships were observed are tabulated in Appendix Table 17. As before, the concentrations of Ca, Mg and Mn were 0.05 meq per liter. Figure 11 illustrates that the effect of increasing Zn concentration was similar to that of Mg and Fe^{++}. Unlike the results of these ions, however, the effect manifested upon the addition of Ca was not as great. A possible reason for this may be seen by comparing Figure 11 with Figures 4 and 9. At the concentrations examined, it is obvious that Zn inhibited Mn absorption to a greater extent than did either Mg or Fe^{++}. Consequently, Zn may have eliminated that portion of the Mn absorption which Ca blocked in conjunction with Mg and Fe^{++}. Further indication of the increased inhibitory effectiveness of Zn is seen in the Mg curve of Figure 11. Whereas Fe^{++} was incapable of reducing Mn absorption below that occurring in the presence of Mg, Zn exerted an additional suppressing effect. It should also be noted that at the highest Zn concentration (0.1 meq/l), both Ca and Mg appeared to exert a slight

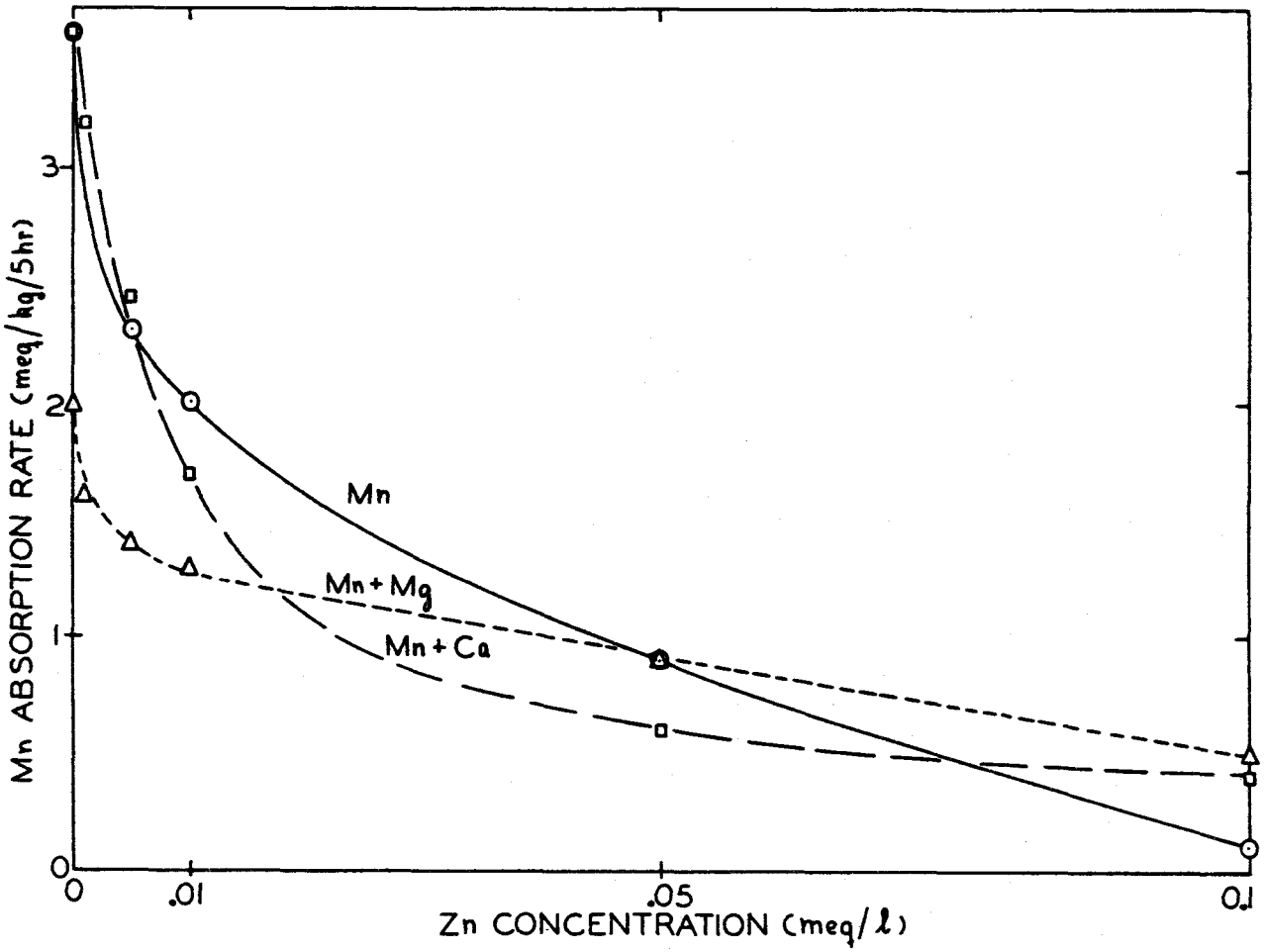

Figure 11. The effects of increasing Zn concentration on the absorption of Mn in the absence and presence of Mg and of Ca at pH five. The concentrations of Mn, Mg and Ca were 0.05 meq per liter. (Experiment 6-101).

protective effect.

In contrast to Fe^{++}, Zn was absorbed very slowly by excised barley roots. This can be seen in Table 11 where some of the data from Appendix Table 17 have been summarized. With single-salt solutions, the rate of Zn absorption was less than one-quarter that of Mn (0.8 compared to 3.6 meq/kg/5 hr). The slow nature of Zn absorption has also been reported recently by Schmid, Haag and Epstein (1965). Nevertheless, their studies with metabolic inhibitors and low temperatures established its dependence on metabolism.

Table 11. Absorption rates of Zn and Mn as influenced by each other in the absence and presence of Ca and of Mg at pH five. The concentrations of all ions were 0.05 meq per liter (Experiment 6-101).

Treatment	Absorption Rate	
	Zn	Mn
	meq/kg/5 hr	
Zn	0.8	
Mn		3.6
Zn + Mn	1.2	0.9
Zn + Mn + Ca	1.4	0.6
Zn + Mn + Mg	1.1	0.9

It is interesting that when these ions are present together at equivalent concentrations (0.05 meq/l), Zn absorption exceeded that of Mn, the rates being 1.2 and 0.9 meq/kg/5 hr, respectively

(Table 11). Although the rates were low, Mn appeared to have a slight stimulatory effect on the absorption of Zn. This was true in the presence of Ca and Mg, also. The fact that Mn absorption from a Zn-Mn solution was greatly reduced, while Zn absorption was increased, would indicate that these two divalent metal ions were not competing for the same carrier. The lack of competitive inhibition of Zn absorption by Mn also was observed by Schmid, Haag, and Epstein (1965). They found little effect from Mn even at concentrations ten times that of Zn in the ambient solution.

Copper. The results of an experiment in which the effect of Cu on Mn absorption was examined are shown in Figure 12. The pernicious nature of Cu is immediately apparent from the net loss of Mn during the five-hour absorption period. Analysis of the K, Ca and Mg status of the roots further substantiated the apparent disintegration of the membrane (see Appendix Table 18). At Cu concentrations of 0.005 meq per liter or greater, considerable losses of K occurred particularly in the absence of Ca. At the higher Cu concentrations, Ca and Mg losses amounted to approximately one-half of their initial content in the roots. These substantial losses of endogenous ions clearly indicate the disruption of the membrane. This is appreciated when one considers that roots lose very little K when placed in distilled water at pH five or six (Fawzy, Overstreet and Jacobson, 1954). The highly

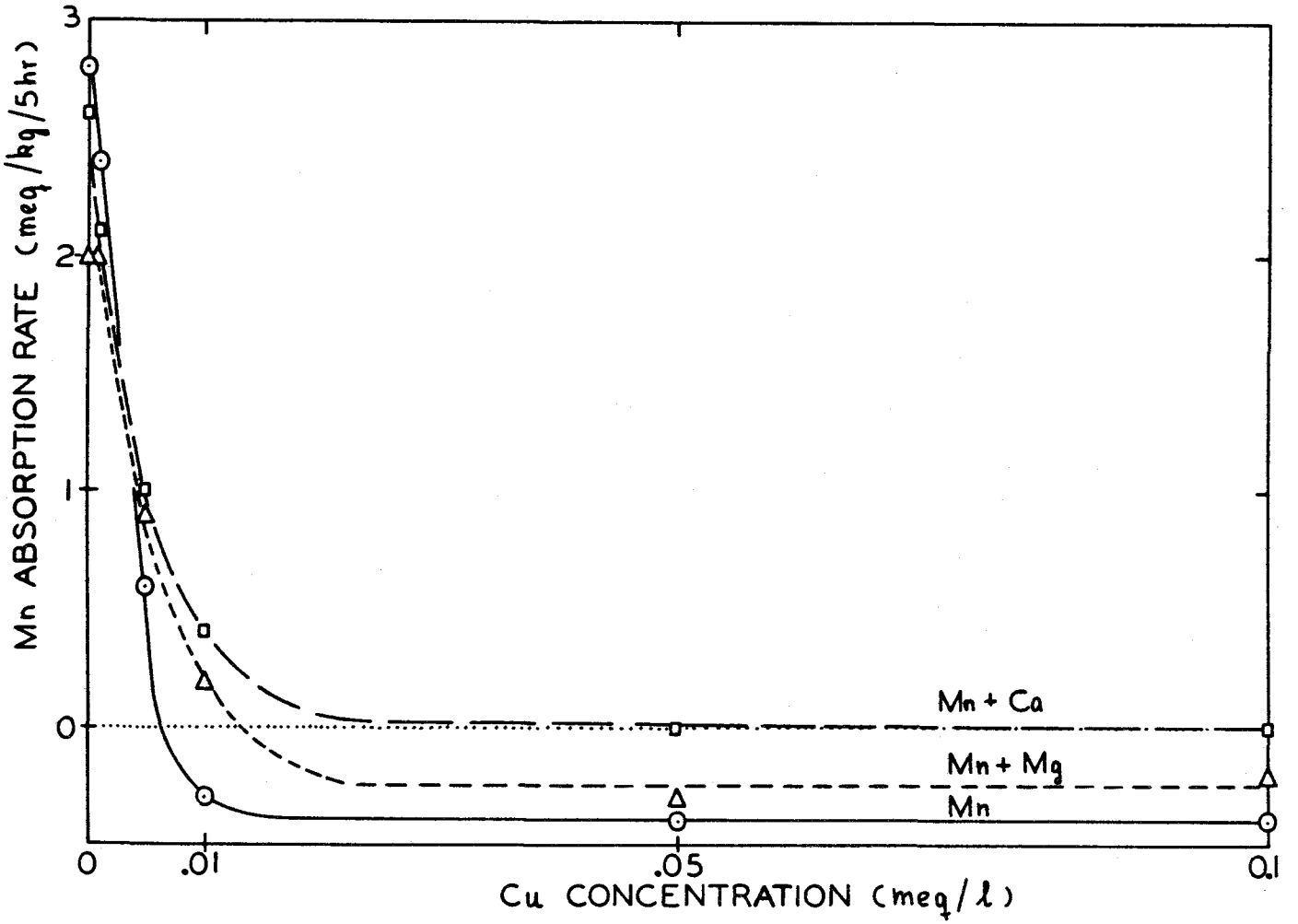

Figure 12. The effects of increasing Cu concentration on the absorption of Mn in the absence and presence of Ca and of Mg at pH five. The concentrations of Mn, Ca and Mg were 0.05 meq per liter. (Experiment 6-105).

detrimental effect of this heavy metal is of interest when compared to the effect of Mn. Whereas as little as 0.005 meq Cu per liter caused large losses of K, it can be seen in Appendix Table 5 that this was not true of Mn even at concentrations as high as 10.0 meq per liter.

It is difficult to determine from this experiment whether direct Cu interference of Mn absorption occurred in view of the impairment of the membrane. If the structural integrity of the membrane was such that large losses of inorganic ions occurred, it is questionable whether the transport mechanism was intact. Even if active transport was occurring, the data was confounded by both the leakiness of the membrane and the resulting change in the composition and concentration of the external solution. Only at 0.001 meq Cu per liter in the presence of Ca was the absorption of Mn reduced without any obvious detrimental effects.

Although the uptake of Cu was appreciable (see Appendix Table 18), it is doubtful that it was metabolically implemented considering the condition of the membrane. Nevertheless, the root material was highly efficient in removing Cu from the solution. This was evident from the measurable uptake from solutions considered free of Cu. It can be seen in Appendix Table 18 that the total six-hour uptake of Cu from the minus-Cu treatments was 0.2 meq per kilogram. This would represent a concentration of

only 0.0002 meq Cu per liter in the ambient solution. Analysis of the distilled water used for the treatment solutions showed that the Cu content was below the detection limit of 0.01 ppm or less than approximately 0.0003 meq per liter.

Aluminum. A study of the regulatory effect of Al revealed an almost complete inhibition of Mn absorption. The data are illustrated in Figure 13, with further details given in Appendix Table 19. Obviously, Al was extremely effective in blocking the absorption of Mn. At equivalent concentrations of Al and Mn, Al suppressed the rate of Mn absorption by nearly 80%. This antagonistic effect of Al on the absorption of Mn has also been observed in excised wheat roots.[4] It was reported that Mn absorption from acidic solutions was severely depressed by small amounts of Al.

In the presence of 0.5 meq Ca per liter, Al inhibition was even more effective. At an Al:Mn ratio of only 1:10, the absorption rate was less than 10% of that from the single-salt Mn solution. At higher Al levels complete inhibition occurred. A second experiment was then designed to examine the effect of Al in a concentration range only one-tenth that of the previous one. At the same time, its effect in the presence of added Mg (0.05 meq/l) was also

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[4]Unpublished data of W. Campbell, D. L. Craig and W. A. Jackson, 1960, reported by Jackson (In press).

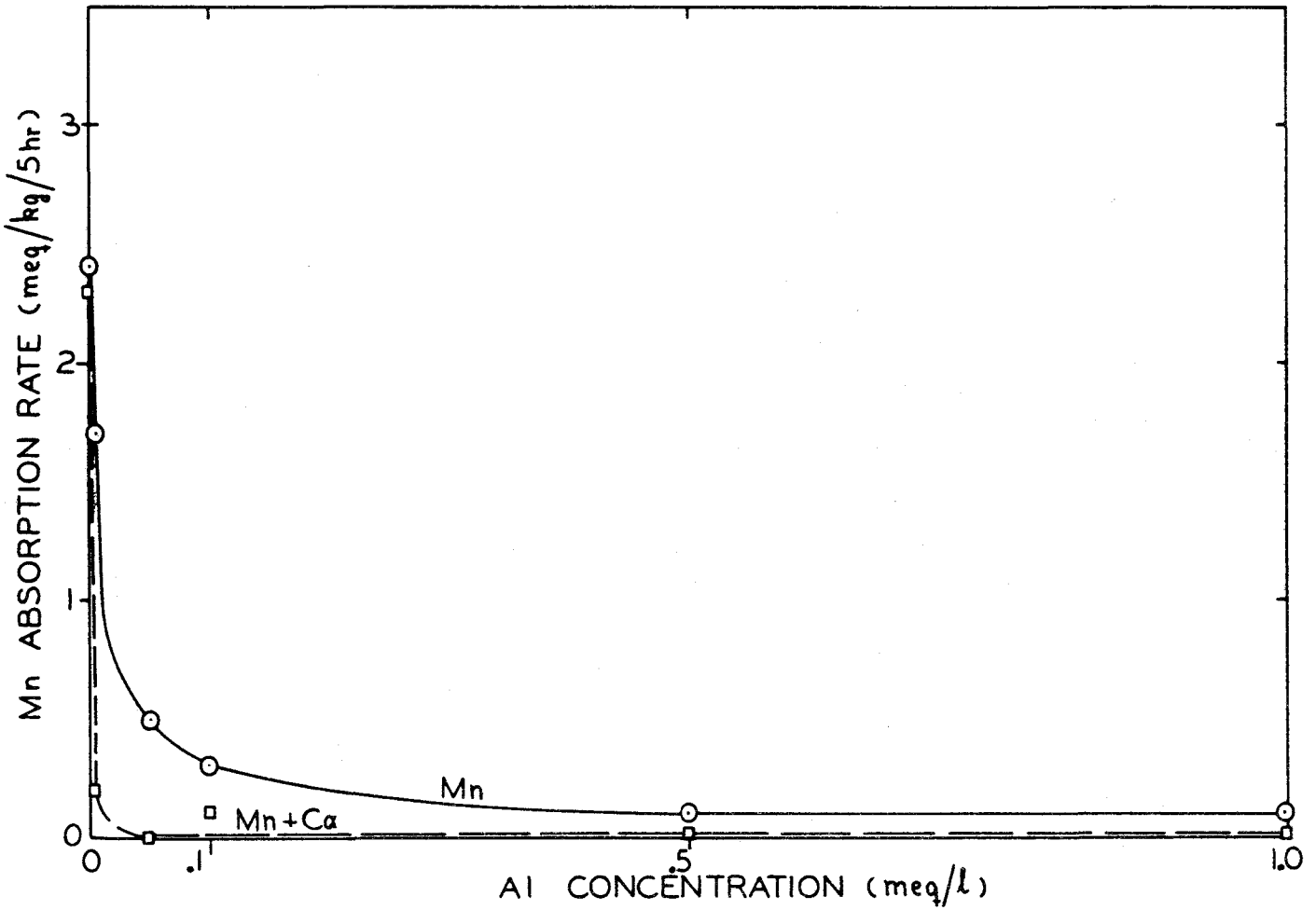

Figure 13. The effects of increasing Al concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-313).

evaluated. The results of the experiment are presented in Figure 14 and Appendix Table 20. Other than the unexpected irregularity at the low concentrations, the effect of Al resembled that in Figure 13 very closely. No explanation is offered for the apparent stimulation by Al following the initial drop in Figure 14. Further study and verification of this phenomenon is necessary. It is noteworthy that the points which were duplicated in the two experiments were very comparable. In the presence of Mg, the effect of Al was essentially the same except that the inhibitory effect was slightly enhanced.

An analysis of the Al content of the roots in the latter experiment indicates that an appreciable uptake of Al occurred (see Appendix Table 20). It is not known, however, if this uptake was wholly non-metabolic or represented some active absorption. Rorison (1965) found that Al uptake by excised sainfoin roots followed the characteristic pattern of rapid initial uptake. However, this phase was not accompanied by a subsequent, linear rate of absorption. It was further observed that the majority of Al was retained when the roots were washed with water, but that a considerable fraction was removed by washing with a buffer solution known to chelate Al. Rorison (1965) concluded, therefore, that most of the Al uptake involved absorption in the Donnan free space. On the basis of the strong affinity of Al for pectin (Joslyn and Luca, 1957), he assumed that Al was bound to the cell walls. Supporting

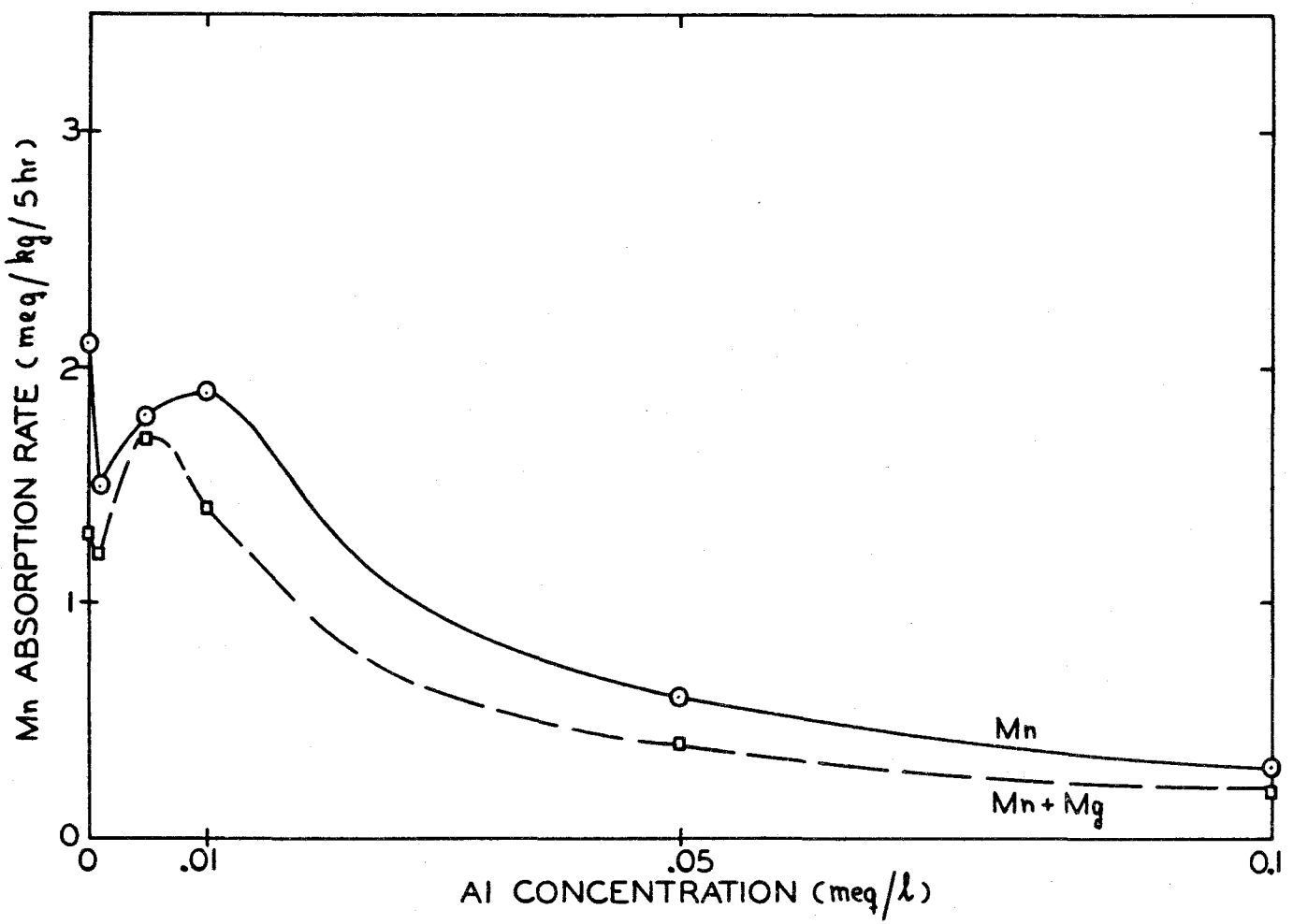

Figure 14. The effects of increasing Al concentration on the absorption of Mn in the absence and presence of Mg at pH five. The concentrations of Mn and Mg were 0.05 meq per liter. (Experiment 6-103).

evidence for this assumption has been furnished by Clarkson (1966) who found that 85 to 95% of the Al in barley roots treated with mM $Al_2(SO_4)_3$ was associated with the cell wall fraction.

Lanthanum. Two similar experiments were subsequently conducted to study the effects of another trivalent ion, La. In the first, La concentrations were varied from 0 to 1.0 meq per liter (see Appendix Table 21). Manganese was present at 0.05 meq per liter and the Ca treatments contained 0.5 meq Ca per liter. In the second experiment, the range of La concentrations was restricted to 0 to 0.1 meq per liter (see Appendix Table 22). The Mn and Mg concentrations were each 0.05 meq per liter. As is apparent in Figures 15 and 16, La exerted an even greater inhibitory effect on Mn absorption than did Al. Neither Ca nor Mg altered this pattern materially.

The exceedingly high sensitivity of Mn to La and Al is especially interesting in view of their effect on K absorption. It has been shown that both La and Al had a pronounced stimulatory effect on the accumulation of K (Jacobson, et al., 1961a; Fawzy, Overstreet and Jacobson, 1954). An experiment in this laboratory also revealed that while Mn absorption was severely inhibited by La, K absorption was greatly enhanced (see Appendix Table 23). As shown in Table 12, K absorption from solutions containing 0.5 meq K per liter was increased over 200% by the presence of 0.05

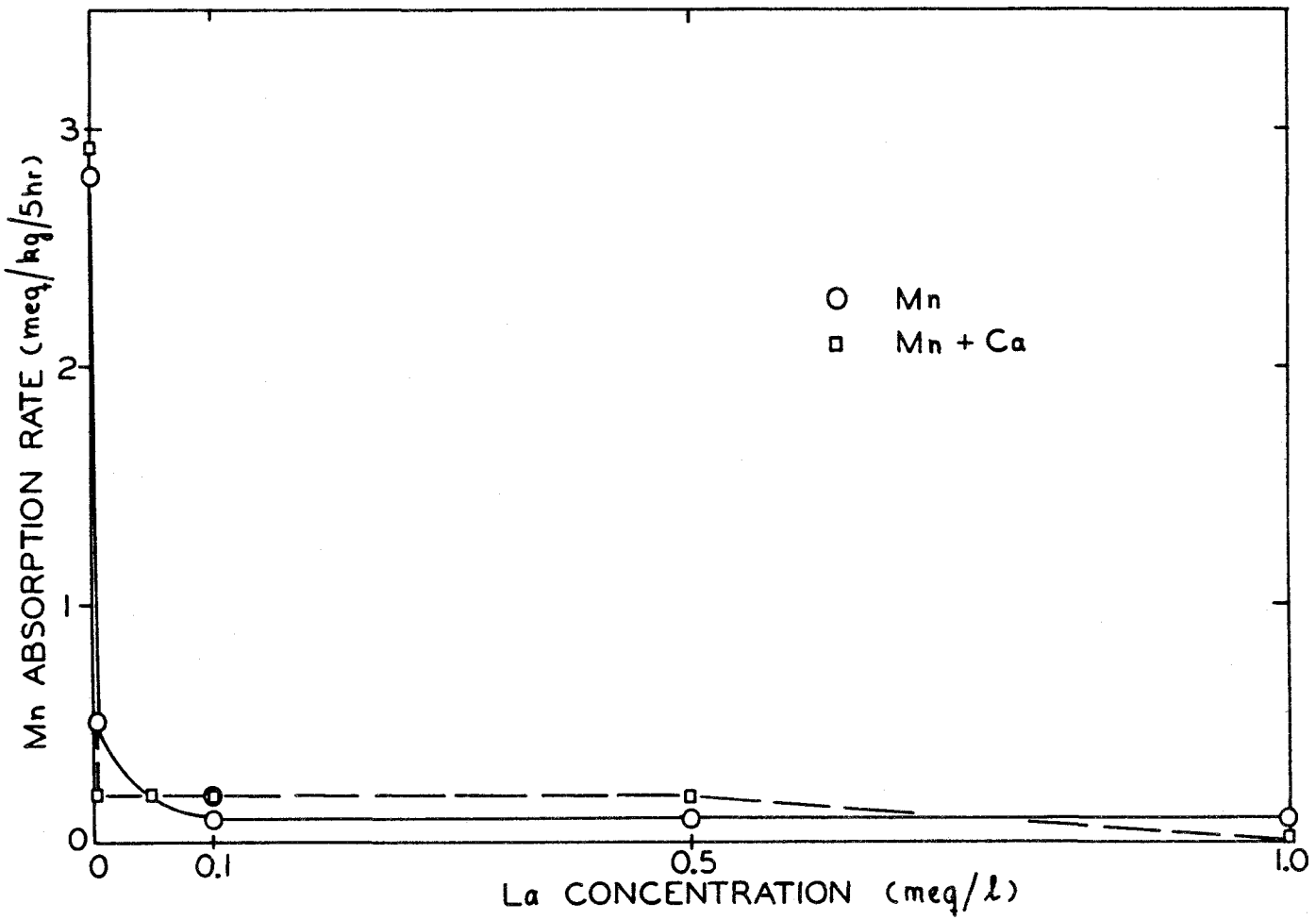

Figure 15. The effects of increasing La concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-317).

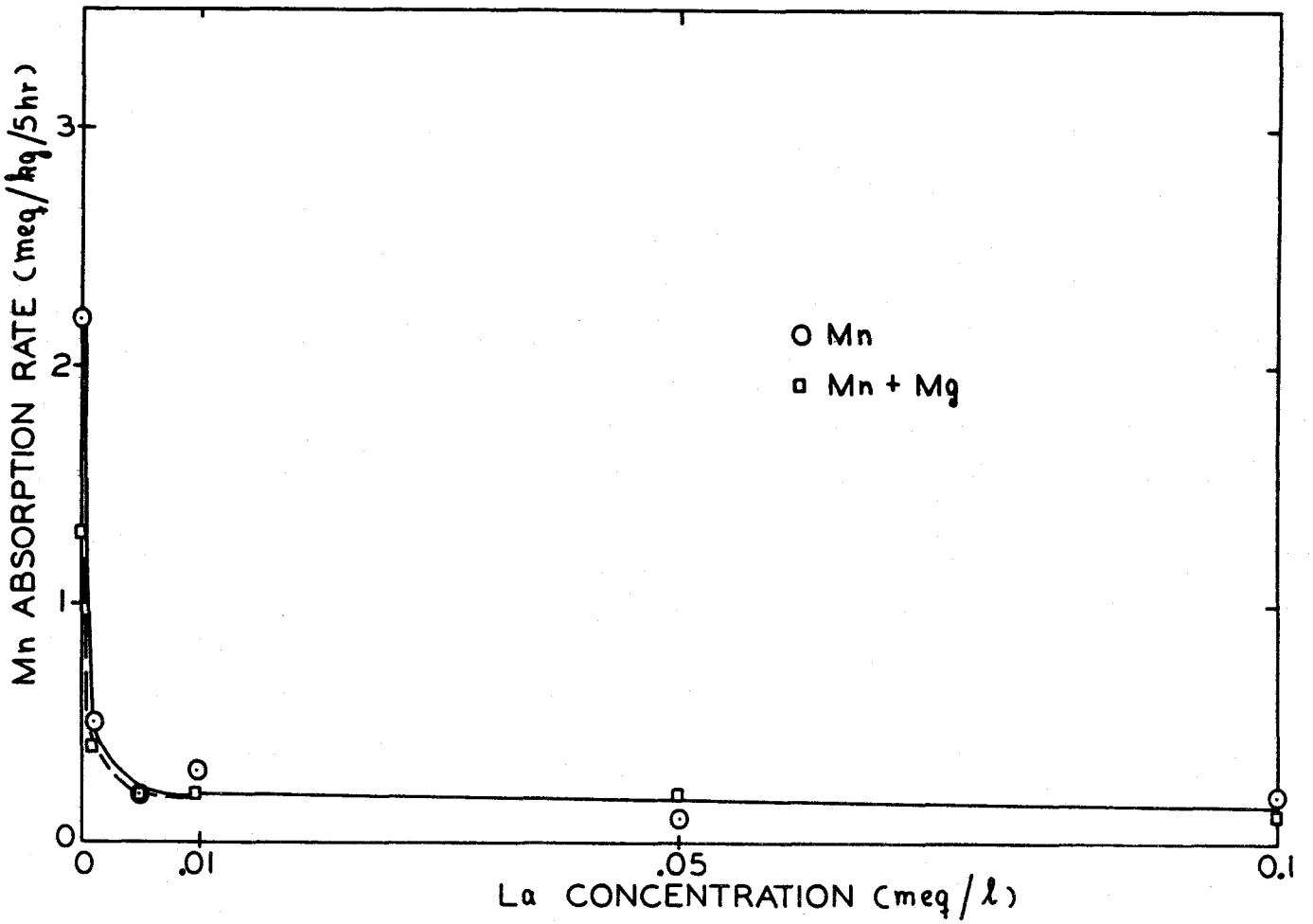

Figure 16. The effects of increasing La concentration on the absorption of Mn in the absence and presence of Mg at pH five. The concentrations of Mn and Mg were 0.05 meq per liter. (Experiment 6-102).

meq La per liter. In contrast, Mn absorption from 0.05 meq $MnCl_2$ per liter was nearly completely blocked by 0.05 meq of La. As illustrated above in Figure 16, even a La:Mn ratio of 1:50 reduced the absorption of Mn over 75%.

Table 12. Absorption rates of Mn and K as influenced by La and various combinations of these ions at pH five. The concentrations of Mn and La were 0.05 meq per liter and that of K was 0.5 meq per liter. (Experiment 6-110).

Treatment	Absorption Rate	
	Mn	K
	meq/kg/5 hr	
Mn	2.8	
K		6.7
Mn + La	0.2	
K + La		13.5
K + Mn	1.2	16.8
K + Mn + La	0.2	13.6

Another interesting observation in Table 12 was the respective stimulations of K absorption by Mn, La and Mn + La treatments. Whereas Mn had a greater stimulatory effect on K absorption than did La, the La effect obviously predominated in the Mn-La system. This is probably due to a stronger attraction for La than for Mn at the reaction site.

Ferric Iron. Because of increased acidity associated with

increasing concentrations of Fe^{+++}, the effects of this trivalent cation could be studied in only a limited concentration range from 0 to 0.01 meq per liter (see Appendix Table 24). The effects of Fe^{+++} were also evaluated in the presence of Ca and of Mg at concentrations of 0.05 meq per liter. The absorption data are presented in Table 13. Quite unexpectedly, the effect of Fe^{+++} was not an inhibitory one. In direct contrast to ferrous-Fe, ferric-Fe in both the absence and presence of Ca slightly promoted the absorption of Mn (compare with Figure 9). Only in the presence of Mg were the effects of Fe^{++} and Fe^{+++} the same, i.e. little or no effect was manifested. A comparison with the other trivalent ions reveals opposing effects, also. In the 0 to 0.01 meq per liter concentration range, La effectively blocked Mn absorption. The results for Al were slightly erratic, but the general effect was also strongly inhibitory.

Table 13. The effects of increasing Fe^{+++} concentration on the absorption of Mn in the absence and presence of Ca and of Mg at pH five. The concentrations of Mn, Ca and Mg were 0.05 meq per liter. (Experiment 5-319).

F^{+++} Concentration	Mn Absorption Rate		
	Control	+Ca	+Mg
meq/l	meq/kg/5 hr		
0.000	2.8	3.0	1.7
0.001	3.2	3.2	1.6
0.005	3.0	3.1	1.7
0.01	3.1	3.2	1.6

Of equal interest to the effect of Fe^{+++} on Mn absorption is the converse relationship. As stated previously, Shim and Vose (1965) found that Mn clearly competed with Fe^{+++} for the Fe absorption sites. In the experiment described here, Appendix Table 24, Mn had no effect on the absorption of Fe. Furthermore, little or no effect was exhibited by Mn + Ca or Mn + Mg treatments. Unfortunately, the metabolic nature of Fe^{+++} uptake by excised barley roots is not well known. Some indication of the role of metabolism in Fe^{+++} uptake was obtained in another experiment (see Appendix Table 2). The uptake of Fe from a solution containing both Mn and Fe^{+++} was determined in the presence of DNP and at 0.5° and 25° C. It was found that Fe uptake was only partially eliminated by DNP and low temperature during the five-hour absorption period. It appears, therefore, that both non-metabolic and metabolic uptake of Fe occurred after the initial one-hour period. Whether the non-metabolic uptake takes longer than one hour for completion or whether Fe precipitation or adsorption occurred throughout the experiment is not known. Also unknown is the valence state of Fe when absorbed. On the basis of the work of Brown, Holmes and Tiffin (1961), Shim and Vose (1965) conceded that the absorption of iron may involve prior reduction of Fe^{+++} to Fe^{++}.

Effects of the Monovalent Cations

A study of the effects of various cations on the absorption of Mn would not be complete without looking at the monovalent ions. Consequently, the effects of K, Rb, Na and Li on Mn absorption were studied separately in several different experiments. In each case, Mn absorption from 0.05 meq per liter $MnCl_2$ solutions was determined as a function of increasing monovalent ion concentrations.

Potassium. In the first experiment, the effect of K was observed at concentrations of 0 to 1.0 meq per liter. The results of this experiment, tabulated in Appendix Table 25, are summarized in Table 14. Somewhat unanticipated, the effect of K closely resembled that of several polyvalent cations. Although not as effective as Mg, K interfered with Mn absorption even at K:Mn ratios of less than one. In view of the similarity between the effects of K and Mg, a second experiment was conducted to determine the influence of K in the presence of Ca (see Appendix Table 26). Although the general absorption rates in this experiment were somewhat lower than usual, the effect of K was still evident. This is shown in Figure 17. Unlike the influence of Mg, the K effect was only slightly accentuated by the presence of Ca. Coincident with the depressive effect of K on Mn absorption, it should be recalled that Mn greatly enhanced the absorption of K. This effect was shown

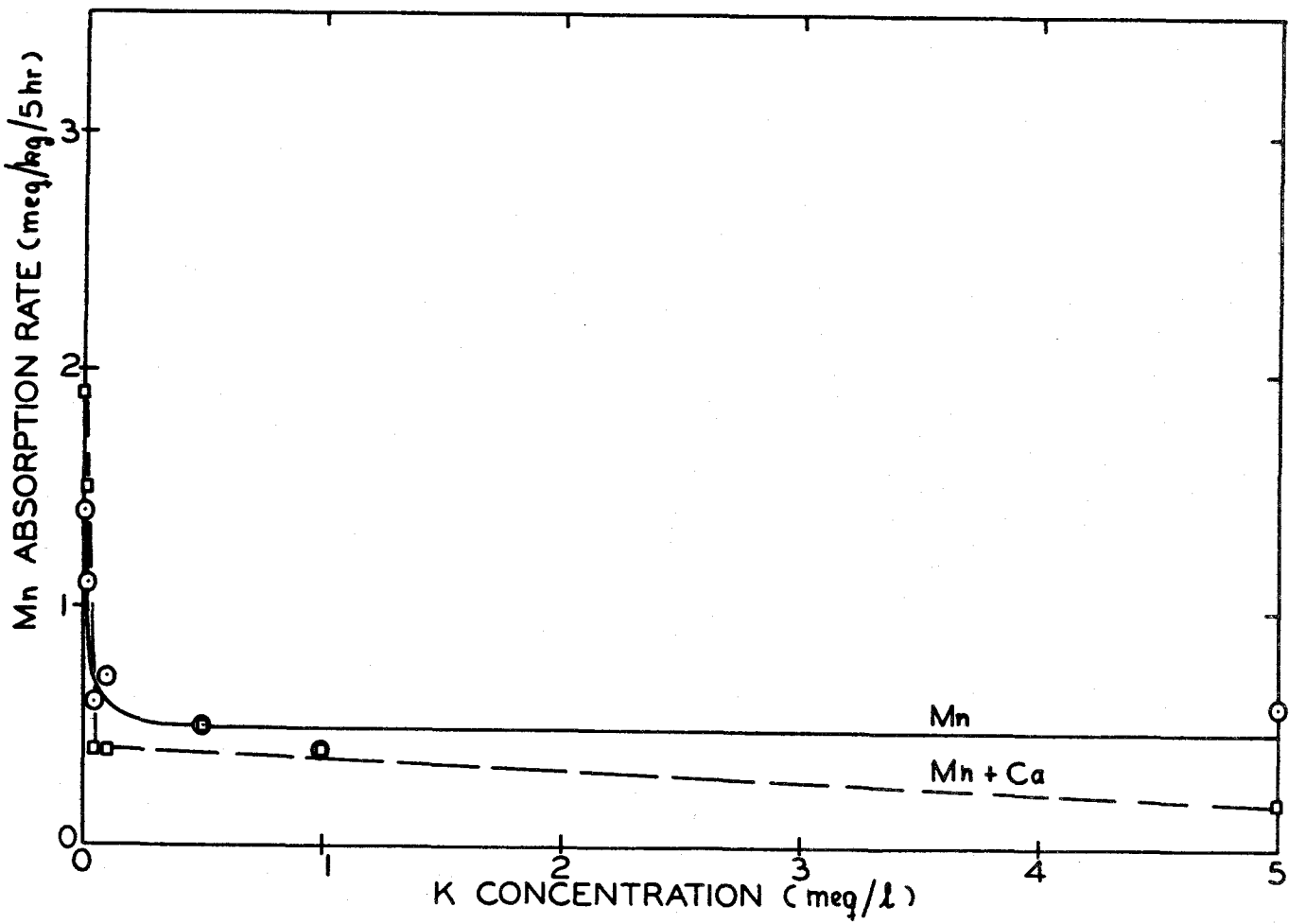

Figure 17. The effects of increasing K concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-36).

above in the two experiments described in Appendix Tables 6 and 23. In Table 12 it was seen that the K absorption rate from 0.5 meq KCl per liter increased from 6.7 to 16.8 meq/kg/5 hr upon the addition of 0.05 meq Mn. This represents a stimulation of over 250%.

Table 14. The effects of increasing K concentration on the absorption of Mn at pH five. Manganese was present at 0.05 meq per liter. (Experiment 5-23).

K Concentration	Absorption Rate	
	Mn	K
meq/l	meq/kg/5 hr	
0.000	3.1	0.2
0.001	3.1	0.7
0.01	2.5	5.1
0.1	1.3	7.7
1.0	0.9	21.8

Rubidium. The nature of the Rb effect, though similar to that of K, had its own peculiarities. Figure 18 illustrates the results of a Rb experiment which is described in Appendix Table 27. In both the absence and presence of 0.5 meq Ca per liter, small additions of Rb had a stimulatory influence on the absorption of Mn. Further additions of Rb resulted in a curve of the same general shape as K. In the presence of Ca, however, the depressive effect of Rb was considerably more pronounced than was that of K. In this respect,

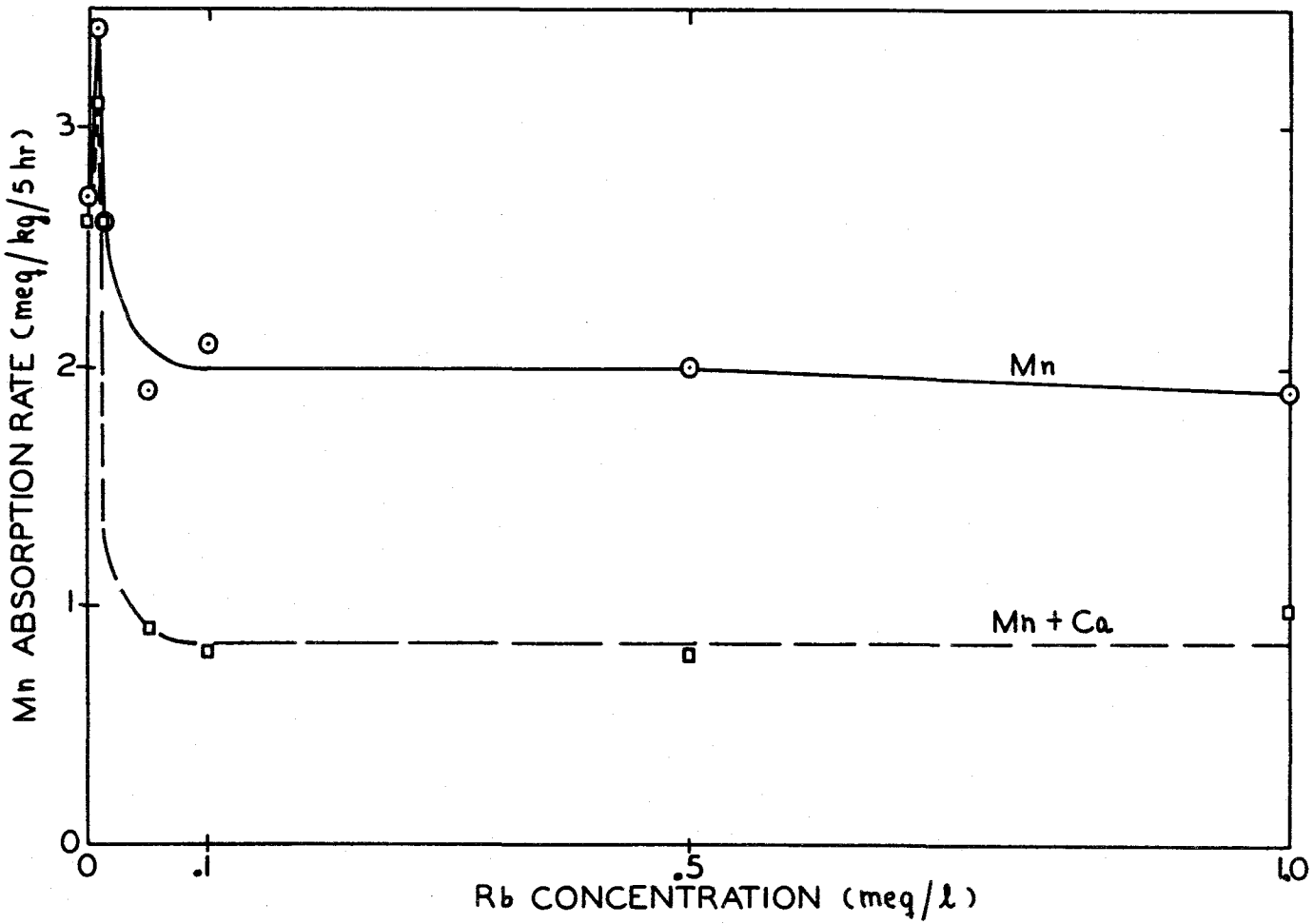

Figure 18. The effects of increasing Rb concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-39).

the effect of Rb more closely resembled that of Mg.

Like K, Rb absorption was markedly stimulated by Mn. This was found in a separate experiment described in Appendix Table 28. The rate of Rb absorption from 0.05 meq RbCl per liter was accelerated from 4.9 to 8.0 meq/kg/5 hr by the addition of an equivalent amount of Mn.

Sodium. The response of Mn absorption to Na was comparable to that of K and Rb. This can be seen in Figure 19 and from the data in Appendix Table 29. As in the case of Rb, a small amount of Na slightly increased the rate of Mn absorption. Unlike the effect of Rb, this did not occur in the presence of Ca, also. The fact that this stimulatory effect was not observed with K is not surprising. Whereas the amount of endogenous Rb and Na was very small, the initial K content of the root material was approximately 20 meq per kilogram. Consequently, the K concentration in the immediate vicinity of the membrane, due to the small loss of K, might be sufficient to obscure any stimulatory effect.

Subsequent to the slight initial increase, a rapid drop in the rate of Mn absorption occurred which was followed by a gradual decline. The increased effect in the presence of Ca was intermediate to that found with K and Rb.

Like the stimulation of K and Rb absorption, Mn greatly enhanced the absorption of Na (see Appendix Table 30). Whereas the

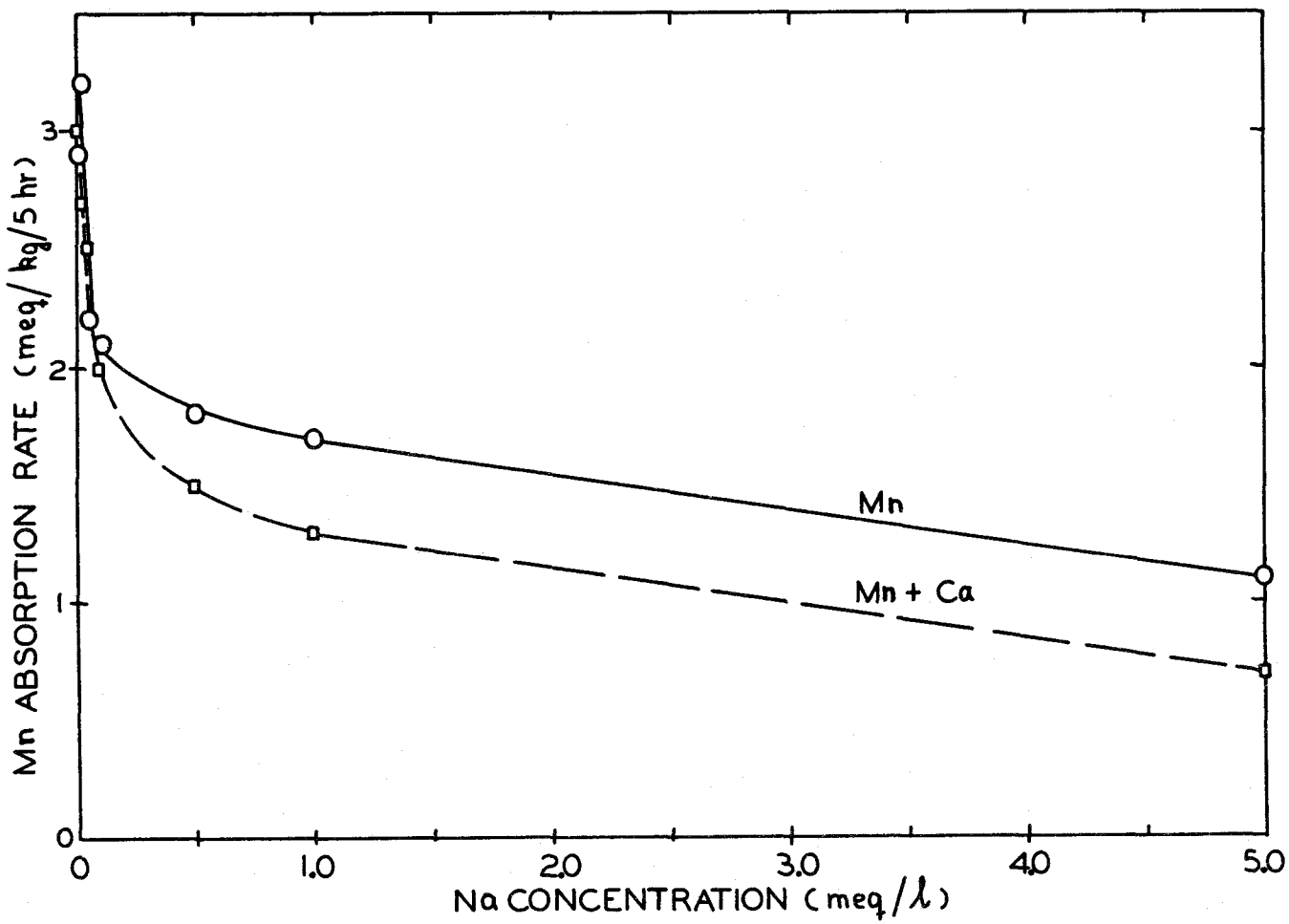

Figure 19. The effects of increasing Na concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-37).

rate of Na absorption from 5×10^{-5} N NaCl was only 0.1 meq/kg/5 hr, it increased to 2.8 meq/kg/5 hr upon the addition of 0.05 meq Mn per liter.

Lithium. The effect of Li on the absorption of Mn was unique among the monovalent cations studied (see Appendix Table 31). Figure 20 reveals a striking stimulation of Mn absorption by increasing concentrations of Li. This result is not surprising, however, in view of the uncommon behavior of Li. Absorption characteristics of Li are different from those of the other alkali cations. Of five alkali metals, only Li uptake was severely inhibited by Ca in the entire pH range from two to eleven (Jacobson, Moore and Hannapel, 1960). In contrast, the uptake of K, Rb and Cs at pH five or less was appreciably greater in the presence of Ca. The differential effect of Ca on Li and Rb uptake was also observed by Epstein (1960). It has since been shown that Li uptake is inhibited by other polyvalent cations as well (Jacobson, et al., 1961a; Waisel, 1962a). Whereas Li uptake was sharply reduced by Ca, Sr, Mn, Al and La, the uptake of K was materially enhanced (Jacobson, et al., 1961a).

It can be seen in Figure 20 that the synergistic effect of Li on Mn absorption resembled the stimulatory effect of Ca (compare with Figure 6). However, the effects of Ca and Li were not additive. Addition of 0.5 meq Ca essentially blocked the enhancement by Li.

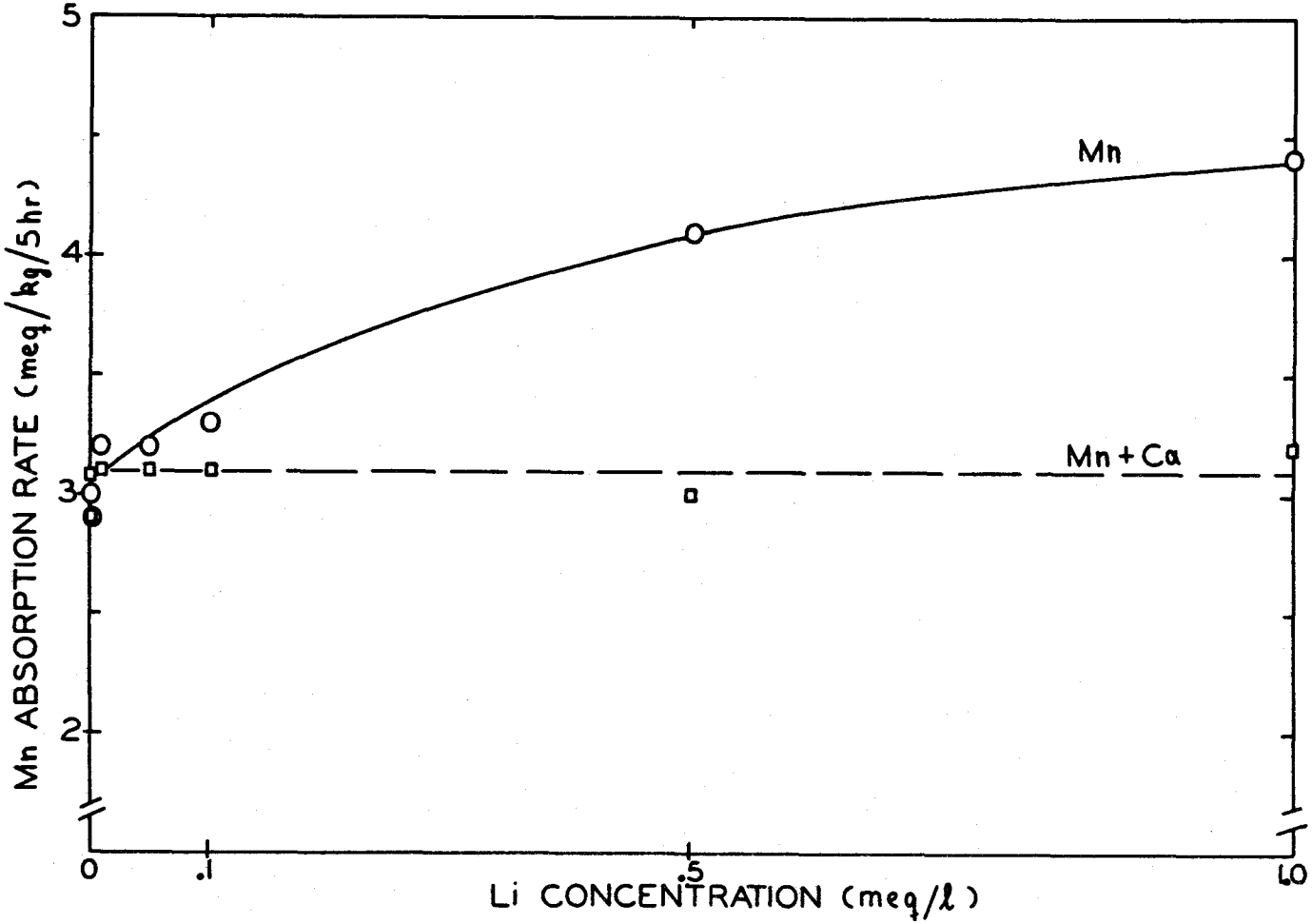

Figure 20. The effects of increasing Li concentration on the absorption of Mn in the absence and presence of Ca at pH five. The concentrations of Mn and Ca were 0.05 and 0.5 meq per liter, respectively. (Experiment 5-310).

A second experiment was designed to ascertain whether Li continued to enhance Mn absorption at a higher concentration (see Appendix Table 32). Also evaluated were the effects of Li in the presence of Ca and of Mg. The concentrations of Mn, Ca and Mg were each 0.05 meq per liter. Table 15 shows that the effect of Li up to 1.0 meq per liter was comparable to the previous experiment. However, a concentration of 10.0 meq Li per liter resulted in a marked reduction of Mn absorption except in the presence of Ca. Apparently, Ca was able to suppress both the stimulatory and inhibitory effects of Li. In the presence of Mg, Li had no effect on Mn up to 1.0 meq per liter. In this case, Li differed from Ca in that it did not enhance the inhibitory effect of Mg.

Table 15. The effects of increasing Li concentration on the absorption of Mn in the absence and presence of Ca and of Mg at pH five. The concentrations of Mn, Ca and Mg were 0.05 meq per liter. (Experiment 6-109).

Li Concentration	Mn Absorption Rate		
	Control	+Ca	+Mg
meq/l	meq/kg/5 hr		
0.000	2.4	2.4	1.6
0.001	2.6	2.2	1.6
0.01	2.5	2.5	1.6
0.1	2.7	2.3	1.6
1.0	3.0	2.9	1.6
10.0	1.3	2.4	1.0

Li absorption, on the other hand, was strongly inhibited by Mn. The absorption rate from 1.0 meq LiCl per liter was depressed over 60% by 0.05 meq of Mn (see Appendix Table 32). The effect of Mn was further examined in a separate experiment described in Appendix Table 33. The absorption of Li from 5.0 meq LiCl per liter was studied as a function of increasing Mn concentrations from 0 to 25 meq per liter. As shown in Table 16, Mn strongly interfered with Li absorption. These data again exemplify the similarity between the effects of Ca and Mn. Lithium absorption, like that of Mg, was highly sensitive to small amounts of either Ca or Mn. Jacobson, et al., (1961a) found that Li uptake was substantially reduced by only 0.1 meq Ca per liter. The data in Table 16 show that Mn was an equally effective inhibitor of Li absorption.

Table 16. The effects of increasing Mn concentration on the absorption of Li at pH five. Lithium was present at 5.0 meq per liter. (Experiment 4-211).

Mn Concentration	Absorption Rate	
	Li	Mn
meq/l	meq/kg/5 hr	
0.0	11.8	0.0
0.1	6.8	5.6
0.5	4.6	9.8
1.0	3.9	11.9
5.0	2.2	13.6
10.0	1.9	14.0
25.0	1.1	15.1

GENERAL DISCUSSION

General Characteristics of Manganese Absorption

The basic aspects of Mn absorption as described in the foregoing sections were, in general, similar to other ions. Like most inorganic cations, Mn was actively absorbed at a relatively rapid rate. Nearly complete inhibition of steady-state Mn absorption by low temperature, DNP, azide and arsenate is strong evidence for metabolically-mediated transport of Mn. This conclusion directly contradicts that obtained by Page and Dainty (1964). The most apparent reason for this discrepancy is the difference in the age and physiological condition of the roots. In the study described in this thesis, roots eight to twelve centimeters long were readily obtained from five-day-old barley seedlings. In contrast, the four-week-old oat roots used by Page and Dainty (1964) were only three to eight centimeters long. Since the oat plants were grown the entire four weeks in a nonaerated media without Mn, it is seriously questioned whether physiologically healthy tissue was obtained. The small amount of growth of the oat roots would support this view. The failure of these authors to detect active Mn absorption was undoubtedly due to the use of an essentially inactive metabolic system. It is difficult to imagine that metabolically-dependent

absorption of Mn is absent in oat roots. This is particularly so in view of the active transport of Mn existing in roots of such closely related species as barley and wheat.[5] Other evidence for metabolic Mn absorption has been obtained for red beets (Skelding and Rees, 1952), yeast (Rothstein, et al., 1958; Jennings, Hooper and Rothstein, 1958) and animal tissue (Chappel, Greville and Bicknell, 1962; Chappel, Cohn and Greville, 1963).

From Figures 2 and 3 it is evident that, within limits, the rate of Mn absorption was strongly dependent upon the hydrogen-ion concentration and the concentration of Mn. No appreciable metabolic absorption occurred below pH four. This was not unexpected in light of the injurious effects of the acidic environment. Considerable losses of cellular constituents are known to occur at pH values of four or less (Jacobson, et al., 1950). In the physiological pH range, absorption increases rapidly with decreasing hydrogen-ion concentration.

The relation between absorption and ambient concentration was essentially logarithmic. A rapid acceleration of absorption with initial increasing concentration was followed by a decreasing rate (per unit concentration) which asymptotically approached a maximum.

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[5] Unpublished data of W. Campbell, D. L. Craig and W. A. Jackson, 1960, reported by Jackson (In press).

When the rate of absorption was no longer a function of concentration, all available transport sites or carriers were considered to be saturated. Manganese toxicity was not considered a factor below concentrations of 5.0 meq per liter in the short-term experiments. As shown in Tables 2 and 3, neither the absorbing capacity of the root nor the rate of respiration was materially impaired at concentrations less than 5.0 meq per liter.

Selective Absorption of Ions

Site of Selectivity

In the study reported here, as well as in many others, the most outstanding observation is the many specific and different effects that ions exert on the absorption of one another. To be effective, it is clear that these ions must be present in the ambient solution. That is, the selective transport of ions across the plant membrane is controlled to a large degree by the nature and concentration of ions present at the extracellular surface of the membrane. The fact that it is the external ionic environment which is important cannot be stressed too strongly. For instance, it was pointed out above that only a very small amount of Ca or Mg added to the test solution exerted a remarkable control over ion absorption. Yet these ions were constituents of the growth media and were

present in the root material at a concentration many times that of the external solution. Of course, it is true that the internal salt content of the tissue may affect the rate and extent of absorption in general (Broyer, 1951). But, unless considerable leakage occurs, the endogenous ions have very little discriminatory effect on ion absorption. In the experiments described in this thesis, the initial content of the root material was relatively low and varied only slightly between experiments. Various studies have shown that, within limits, the selectivity of the transport mechanism was largely independent of previous accumulation or content. Pretreatment in various salt solutions failed to reproduce the effect that the ions exhibited when present in the ambient solution during the uptake period. This was found when roots were pretreated in Mn (see Appendix Table 9), Ca (Viets, 1944; Moore, Overstreet and Jacobson, 1961) and UO_2^{++} (Mason, Moore and Maas, 1966). Furthermore, it has been shown here repeatedly that even when the absorption of a cation was reduced or completely blocked, it still exerted a pronounced regulatory effect (Tables 5, 6, 7, 9 and 12). This is particularly evident for Ca which is absorbed very little if at all by excised barley roots in short-term experiments (Moore, Jacobson and Overstreet, 1961).

Of course, the influence of many internal factors on ion absorption must not be overlooked. It is well known that ion

accumulation is strongly affected by the metabolic activity, age, physiological condition and growth of the plant tissue. However, in the studies reported here and in other short-term experiments, these factors were essentially constant. Consequently, the main variable was the ambient solution composition.

Adopting the widely accepted concept of carrier-mediated ion transport, it is also clear that the carrier must come in contact with the external solution to be operative. The fact that the carrier is exposed to the ionic environment which regulates its specificity is no mere coincidence. Rather, this situation strongly suggests that the action of the ions is on the carrier itself. Of course, there is no question that many of the mutual effects between ions can be explained by competition between them for the same transport sites. However, this obviously does not explain the synergistic and non-competitive interactions occurring between ions. The reactive site in this case is visualized to be at some point other than the actual transport site. Presumably, the cation reacts with the carrier molecule in such a way that it changes the transport properties of the carrier.

Mechanism of Selectivity

The most likely mode of action to explain the regulatory effects of cations could be similar to cation-activation of enzymes. Although

little is known about the precise mechanism, the role of metal cations as enzyme activators is well recognized. Of course, the carrier may or may not be an enzyme. However, this need not be a requirement as any number of proteinaceous or perhaps other compounds would suffice. The nature of the reactive sites or ligands to which activating cations may be bound must remain a matter of speculation until the actual carriers are identified. Some of the possible reactive groups which could complex or bind cations are hydroxyl, carboxyl, amino, guanidine, amide, sulfhydryl, disulfide, indole, imidazole and phenolic groups. On the basis of stability data, some predictions have been made about the selectivity between ligand and cation (Williams, 1959, 1961). Calcium, magnesium and manganous ions preferentially combine with oxygen-anion ligands. Cupric and zinc ions are more likely to be bound with sulfur or nitrogen groups, whereas ferrous ions prefer mixed oxygen-nitrogen ligands. Nevertheless, due to the many factors affecting the stability of metal complexes, the affinity of ligands for all cations cannot be placed into any general order or series.

To explain the manner in which cations function in regulating ion transport, the following proposal is made: By attaching to critical activating sites on the carrier, the cation or cations conceivably bring about a change in the shape or conformation of the carrier itself. As a consequence of this conformational change,

access to potential transport sites would be permitted for some ions and denied to others. Either the number of available transport sites or the affinity of the carrier for a particular ion would increase or decrease as the case may be. In other words, cation-induced changes in the shape of the carrier molecule would control the selectivity in ion absorption. The nature of the structural change and the specificity of the activated carrier would be dependent upon the cation or cations involved. For example, the configuration of the carrier or the alignment of critical groups on the carrier would be different for Ca than for Mg.

The mechanism visualized here is somewhat comparable to that advanced by Koshland, Yankeelov and Thoma (1962) and Koshland (1963) to explain the specificity of enzymes. They proposed that the substrate, by binding to flexible active sites, induces a structural change which leads to proper positioning of catalytic groups.

Evidence for the hypothesis of cation-induced structural and conformational changes in enzymes is increasing. In a very recent review, Evans and Sorger (1966) have summarized the work supporting this function for the univalent cations. Other investigators, utilizing techniques of nuclear magnetic resonance and ultraviolet difference spectroscopy, have shown that Mn and other divalent ions induce conformational changes in pyruvate kinase (Mildvan and Leigh,

1964; Mildvan and Cohn, 1965; Suelter, et al., 1966).

The concept of conformational changes to facilitate ion absorption is not entirely new. Hokin and Hokin (1963) proposed a conformational change in a lipoprotein-type carrier to account for Na-K transport across animal membranes. They presented a scheme whereby reactions of the phosphatidic acid cycle produce Na-specific binding sites on the carrier at the intracellular surface of the membrane. Saturation of these sites with Na leads to further conformational changes so that the Na sites become exposed to the extracellular surface. At this point, a diglyceride kinase reaction causes a third conformational change which destroys the Na site and creates a K site. The cycle is then completed by a K-induced conformational change which transfers K from the outside of the cell to the interior where the system is ready for a second cycle.

It should be noted that in this scheme specific binding sites are produced by reactions of the phosphatidic acid cycle rather than by cations. The only function of cation-induced conformational changes is to facilitate transfer across the membrane. Furthermore, the changes are brought about by the ion being transported and not by some other ion which is controlling the specificity.

As far as is known, the concept of cation-induced conformational changes in the carrier to explain the selectivity in ion transport has never been advanced before. Many of the various

effects exerted by ions on each others' absorption can be explained by this mechanism. It must be kept in mind, however, that competition between ions for the same transport site occurs as well. Consequently, some interactions between ions may be the net result of both a competitive and a regulatory effect. Oftentimes, this may be a concentration-dependent effect, e.g. the Ca-Mn or Li-Mn interactions.

As noted, the particular configuration of the carrier is a function of the activating cation or cations. In some cases, the cation-induced conformational change is relatively non-specific, in others it is highly specific. As a result of the new carrier conformation, transport sites for some ions may be destroyed, while for other ions new or more accessible sites may be created.

Regulatory Effects of Cations

An attempt will now be made to discuss the effects of individual cations (and various combinations) on the absorption process in terms of previous explanations and the present hypothesis.

Viets Effect. A starting point logically seems to be the stimulation of K absorption by Ca and other polyvalent cations first observed by Viets (1944) and confirmed later by many others. Viets (1944) suggested that the synergistic effects of the polyvalent cations were related to their influence on the permeability or the surface

metabolism of the plasmalemma. According to the concept presented here, the stimulatory effect is due to cation-induced conformational changes in the carrier. It is proposed that activation by Ca would provide carriers with greater accessibility to such cations as K, Rb and Cs, resulting in increased transport. The fact that other polyvalent cations exert a similar effect indicates that this activation is not specific for Ca (Fawzy, Overstreet and Jacobson, 1954; Jacobson, et al., 1961a; Viets, 1944). Apparently, most multivalent cations induce similar conformational changes in the carrier with respect to the transport of these alkali cations. In fact, the transport of K, and presumably Rb and Cs, seems to be affected similarly by not only individual polyvalent cations, but by various combinations of cations as well (Tables 9 and 12).

On the basis of enzyme kinetics, Kahn and Hanson (1957) proposed that Ca affected K accumulation in two independent reactions. In the first, Ca increased the affinity between K and its carrier while in the second, Ca non-competitively reduced the rate of metabolic K absorption. Whether the stimulatory or depressive effect predominated, depended upon the plant tissue used. It was noted that other polyvalent cations might function in a similar manner. The concept of increased affinity has also been suggested to explain Ca-enhanced Rb absorption (Tanada, 1962). The explanation advanced by these investigators is also quite tenable with the present

proposal. The increased affinity between the ion and its carrier may well be the result of a conformational change.

Jacobson and associates (Jacobson, Moore and Hannapel, 1960; Jacobson, et al., 1961a; Moore, Overstreet and Jacobson, 1961) considered the stimulating effect of Ca and presumably other polyvalent cations to be due to a blocking of interfering ions. They proposed that Ca controlled the selectivity in the absorption process by modifying the permselectivity of the cell membrane. A similar conclusion was drawn by Waisel (1962b). In light of the hypothesis advanced here, the blocking effect could be due to the particular configuration of the carrier. Its ability to accept the interfering ions would depend upon the presence or absence of Ca (or other polyvalent cations) and the resulting configuration. For example, in the absence of any polyvalent cations, Li appeared to be accepted readily on the K carrier and interfered markedly with K absorption (Jacobson, Moore and Hannapel, 1960). However, in the presence of Ca, Li absorption was completely blocked and the interference with K was eliminated. Potassium, on the other hand, was accommodated to an even greater extent. Parallel effects also exist for the influence of Ca and other polyvalent cations on Na-K and H-K relationships (Jacobson, et al., 1961a; Epstein, 1961). These results seem to fit the hypothesis that a conformational change in the carrier, caused by any one of several polyvalent cations, leads to

greater acceptance of K, Rb and Cs and decreased acceptance of Li, Na and H.

Handley, Metwally and Overstreet (1965a, b) have proposed that Ca has two separate and distinct functions in regulating ion absorption. The first is the stabilization of the plasmalemma. This effect is inhibitory and reduces the rates of ion diffusion to transport sites. The second involves participation of Ca in the metabolic transport mechanism resulting in the stimulatory Viets effect. As already discussed, this stimulatory effect is considered the result of more accessible transport sites on the carrier created in the presence of Ca.

The importance of Ca, and perhaps other polyvalent cations, in maintaining membrane integrity and an impermeable barrier to passive movement of ions should not be overlooked. Calcium has long been known to function in this capacity. This has been further substantiated by recent investigations. Marinos (1962) concluded, from evidence obtained with the electron microscope, that the structural integrity of the various cellular membranes is dependent upon Ca. He found that one of the first signs of Ca-deficiency was the disorganization of the vacuolar and plasma membranes. Van Steveninck (1965) has recently investigated the possible role of other divalent ions such as Mg, Sr, Ba, Fe, Mn, Zn, Cu, Co and Ni in controlling membrane permeability. Of these ions, both Mn

and Sr were capable of substituting for Ca. Other ions were considerably less capable or altogether ineffective. Whereas substitution by Sr is not surprising, it is noteworthy that Mn also had this property. Although Ca, and perhaps other cations, are no doubt essential to the maintenance of the cell membranes, their regulatory influence on selective transport is difficult to explain on this basis alone.

Polyvalent Cation Regulation of Mn Absorption. From the Viets effect it would appear that polyvalent cations reacted similarly via some non-specific mechanism. It was suggested that the absorption of K was promoted by some structural change in the carrier which could be caused by any one or more of a number of polyvalent cations. However, the conformational changes cannot be identical in every respect. This has been well demonstrated by the effects of various cations on Mn absorption. Whereas Ca activation slightly stimulated the absorption of Mn (Figure 6), other polyvalent cations such as Mg, Ba, Fe^{++}, Zn, Cu, Al and La reduced or nearly eliminated Mn transport (Figures 4, 5, 8, 9, 11, 12, 13 and 15, respectively). Strontium and ferric ions had little or no effect (Tables 10 and 13).

The contrasting effect of Ca on Mn and Mg absorption (Figure 6; Moore, Overstreet and Jacobson, 1961) is further supporting evidence that cations have specific effects on the carrier itself. It

is difficult to explain the stimulation of Mn absorption and the inhibition of Mg absorption in any other way. As noted in the results section, the absorption characteristics of these two divalent ions are very similar. Both Mg + Mn were rapidly absorbed from single-salt solutions and behaved similarly as a function of pH. However, on the basis of the nearly complete mutual inhibition of each others' absorption (Tables 4 and 5), two apparently different transport sites were involved. In the presence of Ca these two sites were affected differently, Mg-sites became less accessible and Mn sites became more accessible.

Similarly, the depressing effects of Mn and Mg on the absorption of each other can only be explained on the basis of a reaction with the carrier at some point removed from the transport site. Again, a plausible explanation is a cation-induced modification of the carriers. That is, the conformation of the ion transport carriers in a Mg-Mn system is such that neither Mg nor Mn are readily accommodated.

The effects of Fe^{++} and Zn resembled those of Mg very closely (Figures 9 and 11). However, without knowing the true metabolic nature of Fe absorption, competition between Mn and Fe for the same transport sites cannot be ruled out. In the case of Zn, the effect must be at a point other than a mutual transport site. This is indicated by the lack of Mn interference with Zn absorption

(Schmid, Haag and Epstein, 1965). If Zn and Mn were competing for identical sites, it is not likely that at Mn:Zn concentration ratios of 10:1, the absorption of Mn would be severely depressed while the absorption of Zn was unaffected. It should be mentioned that at 0.1 meq per liter, toxic effects from Zn were a distinct possibility. This was indicated by the protective effect of Ca and Mg (Figure 11) and by the appreciable loss of Mg from the tissue at the highest Zn concentrations (Appendix Table 17).

The complete inhibition of Mn absorption by Cu was most assuredly due to the highly toxic nature of this heavy metal (Figure 12). However, at concentrations below 0.005 meq per liter, competitive and regulatory effects of Cu cannot be ruled out.

The nearly complete lack of Mn absorption in the presence of Al and La (Figures 13 and 15), without any apparent toxic effects, indicates the effectiveness of these cations in inhibiting the transport of Mn. That this was a specific effect on the Mn carrier rather than a general damaging effect to the transport mechanism, as a whole, was substantiated by the unimpaired (in fact, enhanced) absorption of K (Table 11; Jacobson, et al., 1961a).

Further strong evidence for cation-induced changes in the carrier comes from the combined effect of Ca and Mg on Mn absorption. As mentioned in connection with the data shown in Figures 4 and 6, Mn absorption was non-competitively inhibited by Mg and

stimulated by Ca, respectively. In view of the inhibitory effect of Ca on Mg absorption (Moore, Overstreet and Jacobson, 1961), one would expect increased Mn absorption upon addition of Ca to the Mg-Mn system. That is, by blocking Mg, Ca would prevent Mg interference of Mn transport while exerting its own stimulatory influence. However, the effect of Ca in the presence of Mg was just diametrically opposite of that expected. As illustrated in Figures 4 and 5, Mg inhibition of Mn absorption was greatly accentuated in the presence of Ca. Obviously, the combination of Ca and Mg had a greater inactivating effect on the Mn carrier than did Mg alone. Furthermore, absorption of Mg was also slight in this system because of the inhibitory effects of both Ca and Mn and Ca absorption was completely absent. In spite of the nearly complete lack of absorption of divalent cations from the Ca-Mg-Mn system, the transport mechanism was far from inactivated. As can be seen in Table 9, K absorption was greatly enhanced in the presence of Ca, Mg and Mn. This observation is especially important since it emphasizes the fact that both stimulatory and inhibitory effects may be exerted by the same cations at the same time. Since in neither case was mutual competition involved, the point of action must have been at some site other than the actual transport site.

It should be noted that inhibition of Mn absorption by other divalent cations was also greater in the presence than in the absence

of Ca. This can be seen in Figures 9, 11 and 13 for Fe^{++}, Zn and Al, respectively. The increased inhibition of Mn absorption in the presence of Ca lends support to the contention that the action of these cations was similar to that of Mg.

Polyvalent Cation Regulation of Li Absorption. The fact that Mn absorption was affected differently by various polyvalent cations is an important observation. It is one of the few pieces of evidence indicating that the effect of polyvalent cations cannot be generalized. Although some effects are the result of relatively non-specific cation-regulated reactions, in some instances certain cations exert rather unique and specific effects. This has been particularly emphasized in studies of Li absorption. Whereas Li transport was almost completely eliminated by Ca and a number of other polyvalent cations (Sr, Mn, Al and La), Mg had surprisingly little effect (Epstein, 1960; Jacobson, Moore and Hannapel, 1960; Jacobson, et al., 1961a; Waisel, 1962a). A comparison of these polyvalent cation effects with those on Mn absorption vividly illustrates that the regulatory effects of cations are often peculiar to the ion involved. For example, whereas Al and La affected Mn absorption differently than Ca and Sr, they affected Li absorption in the same way. It might be noted here, however, that Epstein (1960) and Waisel (1962a) did not attribute the effects of Ca and Sr to a regulatory role. They believed that the inhibition of Li absorption

by Ca and Sr was that of mutual competition. This is difficult to accept in view of the lack of Ca absorption by this tissue (Moore, Jacobson and Overstreet, 1961).

Differential Inhibition of Na, K and Rb Absorption. As discussed above, Ca exerted a definite influence on the relative absorption of K and Na from a mixture of these two ions (Jacobson, et al., 1961a; Epstein, 1961). A very small amount of Ca was capable of markedly increasing the K/Na absorption ratio by enhancing the absorption of K and decreasing that of Na. Epstein (1961) reported that Ca also controlled the relative amounts of Rb and Na absorbed from mixed systems. He ascribed the role of Ca to its essentiality in maintaining the integrity of the selective transport system. However, his data showed that other divalent cations also functioned in this capacity, albeit slightly less effectively. In contrast, Mg was relatively ineffective. While no mechanism was offered by Epstein (1961) to explain the manner in which Ca and the other cations functioned, his results can easily be interpreted in terms of the carrier-conformation theory. The selective absorption of K and Rb over Na could have been simply that the Ca-activated carrier accepted K and Rb more readily than Na.

Except for the inaction of Mg, polyvalent cations in general appeared to govern the selective absorption of Na, K and Rb in a similar manner. However, recent evidence obtained in this

laboratory has revealed that uranyl (UO_2^{++}) has a regulatory effect which is just the opposite of that of Ca.[6] Whereas UO_2^{++} markedly depressed the absorption of K, Na absorption was either unaffected or slightly stimulated. Consequently, in a mixed system, the K/Na absorption ratio was greatly reduced upon the addition of UO_2^{++}. Similar results were also obtained for the relative absorption of Rb and Na. Of the many polyvalent cations studied, UO_2^{++} alone appeared to inactivate the K and Rb transport sites. The fact that UO_2^{++} affected Na very little indicated that it reacted at specific sites on the carrier rather than interfering with metabolism or the transport mechanism in general. The effect of UO_2^{++}, therefore, is further evidence for the diversity and specificity of effects of the polyvalent cations.

Univalent Cation Regulation of Ion Absorption. Regulatory effects of cations on ion absorption are not limited to the polyvalent cations. As can be seen in Figures 17 through 20, the univalent cations had a marked influence on Mn absorption. In general, the effects of K, Rb and Na were comparable to that of Mg and some other polyvalent cations. One significant difference, however, is that K, Rb and Na absorption was greatly enhanced by Mn,

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[6] Mason, B. J. Department of Soils, Oregon State University, Personal communication, 1966. A portion of these results has been reported by Mason, Moore and Maas (1966).

oftentimes more than doubled, whereas Mg absorption was markedly reduced. In the Mg-Mn system, mutual competition was not evident and it may not have been involved in the alkali cation-Mn system either. That is, interactions between two ions whereby the absorption of one ion is stimulated while the other is suppressed is hardly indicative of mutual competition for the same carrier. Nevertheless, these facts do not preclude this possibility. The existence of mutual competition between a monovalent ion and a divalent ion when the absorption of the former is enhanced and the latter reduced has been suggested before. Moore (1960) demonstrated that under certain conditions Mg and the alkali metals were mutually competitive. It was pointed out that this fact is often obscured by the Viets effect.

The possibility that the alkali cations reduce the absorption of Mg and Mn by causing specific conformational changes in the Mg and Mn carriers does exist, however. The fact that Ca accentuated the inhibitory effect of these univalent cations can be used to support either theory. By having a greater stimulatory effect on K and Rb than on Mn absorption, Ca would increase the absorption of K or Rb relative to Mn. Consequently, if these ions were mutually competing, the absorption of Mn would decrease. On the other hand, the combined effects of Ca and the alkali cations may have a greater effect on the Mn carrier than either K, Rb or Na alone. The effect would be comparable to that of Ca-Mg on Mn absorption. In fact,

this explanation better fits the action of Na in the presence of Ca. Calcium does not enhance the absorption of Na in the physiological pH range (Jacobson, Moore and Hannapel, 1960), but does stimulate Mn absorption. Therefore, it is difficult to conceive why the effect of Na would be accentuated in the presence of Ca if Na and Mn were competing for the same transport site.

The effect of Li on ion absorption provides still another example of the non-competitive regulatory effects of one cation on the absorption of another. As shown in Figure 20, Li, up to one meq per liter, increased the rate of Mn absorption to a great extent. In fact, the synergistic effect of Li on Mn absorption was even greater than that of Ca. Although the effects of Ca and Li in this instance were similar, they were not additive. Furthermore, it is apparent from a comparison of their effects on the absorption of other ions that their actions were different. Unlike the effect of Ca, Li was not an effective inhibitor of Mg absorption nor was it capable of stimulating the absorption of K on its own accord (Jacobson, Moore and Hannapel, 1960). It might be noted that Epstein (1962) has reported that in the presence of Ca, Li stimulated the absorption of Rb. These divergent effects of Li add to the considerable other evidence that cations exert specific effects on the transport carriers.

General Remarks

The many diverse and specific effects that cations impose on the ion absorption mechanism support the hypothesis that selective transport results from specific cation activation of the carrier. It is difficult to explain the unique effects of individual cations and certain combinations of cations in any other way. That the cations affect the carrier itself rather than some internal metabolic reaction is evidenced by the fact that the cations are only effective when present in the external solution. It seems imperative that the carrier is exposed to this external ionic environment. When the mutual effects of cations cannot be explained by competition for similar transport sites, their action must be at some other critical point on the carrier. As a consequence of the reaction between cation and carrier, the properties of the carrier are changed in such a manner that transport sites may become either more or less available for a given ion. One of the most feasible mechanisms to explain this reaction is that of cation-induced changes in the conformation of the carrier. The rapidly increasing evidence that cations alter the properties and structure of enzymes provides considerable support for this proposal.

The possibility that ion absorption is implemented by several carriers in no way affects the validity of the hypothesis advanced

here. Whether one or more carriers exist, the regulatory effect of cations remains the same.

SUMMARY

Short-term absorption studies with excised barley roots have revealed that the basic aspects of Mn uptake and absorption were similar to other inorganic cations. A characteristic two-phase course of uptake was found. Following a rapid initial movement into the free space of the root, Mn was absorbed at a slower steady-state rate for several hours. This second phase of absorption was shown to be metabolically mediated. The rate of Mn absorption was essentially a logarithmic function of the ambient concentration up to five meq Mn per liter. Like other cations, the active transport of Mn was inversely related to the hydrogen-ion concentration in the physiological pH range.

An evaluation of the influence of various cations on Mn absorption has revealed several specific regulatory effects. Of the alkali cations studied, Li alone had a pronounced stimulatory effect while Na, K and Rb markedly reduced the absorption of Mn. The alkaline earth cations also exerted widely differing effects. Calcium appeared to promote the absorption of Mn, whereas Mg had a highly inhibitive effect. The combination of both Ca and Mg was even more inhibitory. Strontium apparently was without either effect and Ba had a moderately depressive effect. Other polyvalent cations which were effective inhibitors of Mn absorption were Fe^{++}, Zn, Cu, Al

and La. In contrast, Fe^{+++} was virtually without effect.

The converse relationship showed that Mn effectively blocked the absorption of Li and Mg, but greatly enhanced that of Na, K and Rb.

To explain these diverse regulatory effects, as well as many others reported in the literature, the following hypothesis was advanced: the cationic environment at the extracellular surface of the membrane is believed to control the specificity of the ion carrier. By attaching to critical activation sites, cations induce conformational changes in the carrier which modifies its selective transport properties. The accessibility or affinity of transport sites for a given ion would depend on the particular configuration of the carrier. This mechanism, together with the essentiality of cations in maintaining the stability of the membrane and the mutual competition between some ions for the same transport site, would explain most, if not all, of the regulatory effects exerted by cations on the ion absorption process.

BIBLIOGRAPHY

Brown, J. C. and W. E. Jones. 1962. Absorption of Fe, Mn, Zn, Ca, Rb, and phosphate ions by soybean roots that differ in their reductive capacity. Soil Science 94:173-179.

Brown, J. C., R. S. Holmes and L. O. Tiffin. 1961. Iron chlorosis in soybeans as related to the genotype of rootstalk: 3. Chlorosis susceptibility and reductive capacity at the root. Soil Science 91:127-132.

Broyer, T. C. 1951. The nature of the process of inorganic solute accumulation in roots. In: Mineral nutrition of plants, ed. by Emil Truog. Madison, The University of Wisconsin Press. p. 187-249.

Chappell, J. B., Mildred Cohn and G. D. Greville. 1963. The accumulation of divalent ions by isolated mitochondria. In: Energy-linked functions of mitochondria, ed. by B. Chance. New York, Academic Press. p. 219-231.

Chappell, J. B., G. D. Greville and K. E. Bicknell. 1962. Stimulation of respiration of isolated mitochondria by manganese ions. Biochemical Journal 84:61P.

Clarkson, David T. 1966. Effect of aluminum on the uptake and metabolism of phosphorus by barley seedlings. Plant Physiology 41:165-172.

Dale, J. E. and J. F. Sutcliffe. 1959. The effects of aqueous extracts of red beet root on salt accumulation and respiration of discs of red beet root. Annals of Botany, n. s. 23:1-21.

David, D. J. 1960. The determination of exchangeable sodium, potassium, calcium and magnesium in soils by atomic-absorption spectrophotometry. Analyst 85:495-503.

Epstein, Emanuel. 1960. Calcium-lithium competition in absorption by plant roots. Nature 185:705-706.

_____. 1961. The essential role of calcium in selective cation transport by plant cells. Plant Physiology 36:437-444.

Epstein, E. 1962. Mutual effects of ions in their absorption by plants. Agrochimica 4:293-322.

Evans, Harold J. and George J. Sorger. 1966. Role of mineral elements with emphasis on the univalent cations. Annual Review of Plant Physiology 17:47-76.

Fawzy, Hussein, Roy Overstreet and Louis Jacobson. 1954. The influence of hydrogen ion concentration on cation absorption by barley roots. Plant Physiology 29:234-237.

Handley, Raymond and Roy Overstreet. 1961. Uptake of calcium and chlorine in roots of Zea mays. Plant Physiology 36:766-769.

_____. 1963. Uptake of strontium by roots of Zea mays. Plant Physiology 38:180-184.

Handley, Raymond, Abdel Metwally and Roy Overstreet. 1965a. Divalent cations and the permeability to Na of the root meristem of Zea mays. Plant and Soil 22:200-206.

_____. 1965b. Effects of Ca upon metabolic and non-metabolic uptake of Na and Rb by root segments of Zea mays. Plant Physiology 40:513-520.

Handley, Raymond, Ramon Dios Vidal and Roy Overstreet. 1960. Metabolic and non-metabolic uptake of sodium in roots of Zea mays. Plant Physiology 35:907-912.

Harvey, H. W. 1947. Manganese and the growth of phytoplankton. Journal of the Marine Biological Association of the United Kingdom, n. s. 26:562-579.

Hewitt, E. J. 1963. The essential nutrient elements: Requirements and interactions in plants. In: Plant physiology, a treatise, ed. by F. C. Steward. Vol. 3. New York, Academic Press. p. 137-360.

Hoagland, D. R. and T. C. Broyer. 1940. Hydrogen-ion effects and the accumulation of salt by barley roots as influenced by metabolism. American Journal of Botany 27:173-185.

Hokin, Lowell E. and Mabel R. Hokin. 1963. Phosphatidic acid metabolism and active transport of sodium. Federation Proceedings 22:8-18.

Hooymans, J. J. M. 1964. The role of calcium in the absorption of anions and cations by excised barley roots. Acta Botanica Neerlandica 13:507-540.

Jackson, William. A. (In press). Physiological effects of soil acidity. In: Soil acidity and liming, ed. by R. W. Pearson and F. R. Adams. (American Society of Agronomy. Agronomy, a series of monographs, vol. 11)

Jacobson, Louis, David P. Moore and Raymond J. Hannapel. 1960. Role of calcium in absorption of monovalent cations. Plant Physiology 35:352-358.

Jacobson, Louis, et al. 1950. A study of potassium absorption by barley roots. Plant Physiology 25:639-647.

_____. 1957. The effect of pH and temperature on the absorption of potassium and bromide by barley roots. Plant Physiology 32:658-662.

_____. 1961a. Influence of calcium on selectivity of ion absorption process. Plant Physiology 36:58-61.

_____. 1961b. Effect of root to solution ratio in ion absorption experiments. Plant Physiology 36:62-65.

Jennings, D. H., D. C. Hooper and A. Rothstein. 1958. The participation of phosphate in the formation of a "carrier" for the transport of Mg^{++} and Mn^{++} ions into yeast cells. Journal of General Physiology 41:1019-1026.

Joslyn, M. A. and Guido de Luca. 1957. The formation and properties of aluminum pectinates. Journal of Colloid Science 12:108-130.

Kahn, J. S. and J. B. Hanson. 1957. The effect of calcium on potassium accumulation in corn and soybean roots. Plant Physiology 32:312-316.

Knauss, H. J. and J. W. Porter. 1954. The absorption of inorganic ions by Chlorella pyrenoidosa. Plant Physiology 29:229-234.

Koshland, D. E., Jr. 1963. Correlation of structure and function in enzyme action. Science 142:1533-1541.

Koshland, D. E., Jr., John A. Yankeelov, Jr. and John A. Thoma. 1962. Specificity and catalytic power in enzyme action. Federation Proceedings 21:1031-1038.

Laine, Torsten. 1934. On the absorption of electrolytes by the cut roots of plants and the chemistry of plant exudation sap. Acta Botanica Fennica 16:1-64.

Laties, George G. 1959. Active transport of salt into plant tissue. Annual Review of Plant Physiology 10:87-112.

Lundegardh, H. 1932. Die Nahrstoffaufnahme der Pflanze. Jena, G. Fischer. 374 p.

Marinos, Nicos G. 1962. Studies on submicroscopic aspects of mineral deficiencies. I. Calcium deficiency in the shoot apex of barley. American Journal of Botany 49:834-841.

Mason, Benjamin J., David P. Moore and Eugene V. Maas. 1966. Selective inhibition of cation absorption by uranyl. Nature 209:318-319.

Mildvan, Albert S. and Mildred Cohn. 1965. Kinetic and magnetic resonance studies of the pyruvate kinase reaction. I. Divalent metal complexes of pyruvate kinase. Journal of Biological Chemistry 240:238-246.

Mildvan, Albert S. and Robert A. Leigh. 1964. Determination of co-factor dissociation constants from the kinetics of inhibition of enzymes. Biochimica et Biophysica Acta 89: 393-397.

Moore, David Paul, Jr. 1960. Uptake of calcium and magnesium by excised barley roots. Ph. D. thesis. Berkeley, University of California. 51 numb. leaves.

Moore, David P., Louis Jacobson and Roy Overstreet. 1961. Uptake of calcium by excised barley roots. Plant Physiology 36:53-57.

Moore, David P., Benjamin J. Mason and E. V. Maas. 1965. Accumulation of calcium in exudate of individual barley roots. Plant Physiology 40:641-644.

Moore, David P., Roy Overstreet and Louis Jacobson. 1961. Uptake of magnesium and its interaction with calcium in excised barley roots. Plant Physiology 36:290-295.

Munns, D. N., L. Jacobson and C. M. Johnson. 1963. Uptake and distribution of manganese in oat plants. II. A kinetic model. Plant and Soil 19:193-204.

Nason, Alvin and William D. McElroy. 1963. Modes of action of the essential mineral elements. In: Plant physiology, a treatise, ed. by F. C. Steward. Vol. 3. New York, Academic Press. p. 451-536.

Nielsen, T. R. and Roy Overstreet. 1955. A study of the role of the hydrogen ion in the mechanism of potassium absorption by excised barley roots. Plant Physiology 30:303-309.

Ordin, Lawrence and Louis Jacobson. 1955. Inhibition of ion absorption and respiration in barley roots. Plant Physiology 30:21-27.

Page, E. R. 1961. Location of manganese taken up in short-term absorption by oat roots. Nature 189:597.

Page, E. R. and J. Dainty. 1964. Manganese uptake by excised oat roots. Journal of Experimental Botany 15:428-443.

Parr, J. F. and A. G. Norman. 1963. A procedure for control of pH in cation uptake studies with excised barley roots. Soil Science Society of America Proceedings 27:531-534.

Pollard, Arthur L. and Peter Byrd Smith. 1951. The adsorption of manganese by algal polysaccharides. Science 114:413-414.

Rees, W. J. 1949. The salt relations of plant tissues. IV. Some observations on the effect of the preparation of storage tissue on its subsequent absorption of manganese chloride. Annals of Botany, n. s. 13:29-51.

Roberts, Richard B. and Elaine Aldous. 1951. Manganese metabolism of Escherichia coli as related to its mutagenic action. Cold Spring Harbor Symposia on Quantitative Biology 16:229-231.

Rorison, I. H. 1965. The effect of aluminum on the uptake and incorporation of phosphate by excised sainfoin roots. New Phytologist 64:23-27.

Rothstein, A. et al. 1958. The active transport of Mg^{++} and Mn^{++} into the yeast cell. Journal of General Physiology 41:585-594.

Schmid, Walter E., H. P. Haag and Emanuel Epstein. 1965. Absorption of zinc by excised barley roots. Physiologia Plantarum 18:860-869.

Shim, S. C. and P. B. Vose. 1965. Varietal differences in the kinetics of iron uptake by excised rice roots. Journal of Experimental Botany 16:216-232.

Skelding, A. D. 1957. The effect of carbon dioxide on the absorption of manganese by root tissues of red beet. Annals of Botany, n. s. 21:121-141.

Skelding, A. D. and W. J. Rees. 1952. An inhibitor of salt absorption in the root tissues of red beet. Annals of Botany, n. s. 16:513-529.

Stiles, Walter and K. W. Dent. 1946. The salt relations of plant tissues. III. Further observations on the absorption of manganese chloride by storage tissue. Annals of Botany, n. s. 10:203-222.

Stiles, Walter and A. D. Skelding. 1940. The salt relations of plant tissues. II. The absorption of manganese salts by storage tissue. Annals of Botany, n. s. 4:673-700.

Suelter, C. H. et al. 1966. Studies on the interaction of substrate and monovalent and divalent cations with pyruvate kinase. Biochemistry 5:131-139.

Tanada, T. 1962. Localization and mechanism of calcium stimulation of rubidium absorption in the mung bean root. American Journal of Botany 49:1068-1072.

Tromp, J. 1962. Interactions in the absorption of ammonium, potassium and sodium ions by wheat roots. Acta Botanica Neerlandica 11:147-192.

Umbreit, W. W., R. H. Burris and J. F. Stauffer. 1964. Manometric techniques, 3d ed. Minneapolis, Minn., Burgess Publishing Co. 338 p.

Van Steveninck, R. F. M. 1965. The significance of calcium on the apparent permeability of cell membranes and the effects of substitution with other divalent ions. Physiologia Plantarum 18:54-69.

Viets, Frank G., Jr. 1944. Calcium and other polyvalent cations as accelerators of ion accumulation by excised barley roots. Plant Physiology 19:466-480.

Waisel, Yoav. 1962a. The absorption of Li and Ca by barley roots. Acta Botanica Neerlandica 11:56-68.

_____. 1962b. The effect of Ca on the uptake of monovalent ions by excised barley roots. Physiologia Plantarum 15:709-724.

Weed, Robert I. and Aser Rothstein. 1960. The uptake of divalent manganese ion by mature normal human red blood cells. Journal of General Physiology 44:301-314.

Williams, D. Emerton and James Vlamis. 1957. Manganese toxicity in standard culture solutions. Plant and Soil 8:183-193.

Williams, R. J. P. 1959. Coordination, chelation and catalysis. In: The enzymes, ed. by P. D. Boyer, H. Lardy and K. Myrback. Vol. 1. New York, Academic Press. p. 391-441.

_____. 1961. Nature and properties of metal ions of biological interest and their coordination compounds. Federation Proceedings 20:5-14.

APPENDIX

Appendix Table 1. Conditions, Treatments and Results of Experiment 5-41. The pH was 5.0 ± 0.1 and the temperature was 25 ± 0.5°C. Initial Mn and Ca content of the root material was < 0.1 and 2.7 meq/kg respectively.

Trmt. No.	Time	Trmt. Soln. Composition	Uptake	Absorption Rate
		$MnCl_2$	Mn	Mn
	hour	meq/liter	meq/kg	meq/kg/5hr
1	.25	0.05	1.3	
2	.50	0.05	1.6	
3	1	0.05	1.9	
4	2	0.05	2.4	
5	3	0.05	2.9	
6	4	0.05	3.3	
7	5	0.05	3.8	
8	6	0.05	4.5	2.6
9	8	0.05	5.4	
10	10	0.05	6.6	

Appendix Table 2. Conditions, Treatments and Results of Experiment 6-104. The pH was 5.0 ± 0.2. The temperature was maintained between 24.5 and 25°C for treatments 1 - 16 and 0 - 1.0°C for treatments 17 - 24. Initial Mn, Ca, Li, Fe and K content of the root material was < 0.1, 2.6, < 0.1, 0.3 and 19.0 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition					Uptake					Absorption Rate				
		Mn	Ca	Li	Fe+++	DNP	Mn	Ca	Li	Fe	K	Mn	Ca	Li	Fe	K
	hour	meq/liter				M.	meq/kg					meq/kg/5hr				
1	1	0.05	-0-	-0-	-0-	-0-	2.0				-1.1					
2	6	0.05	-0-	-0-	-0-	-0-	4.6				-2.2	2.6				-1.1
3	1	0.05	0.05	-0-	-0-	-0-	1.2	-0.1			-1.1					
4	6	0.05	0.05	-0-	-0-	-0-	3.7	0.0			-0.7	2.5	0.1			0.4
5	1	0.05	-0-	0.05	-0-	-0-	2.1		0.5		-1.1					
6	6	0.05	-0-	0.05	-0-	-0-	4.4		0.5		-1.8	2.3		0.0		-0.7
7	1	0.05	-0-	-0-	0.01	-0-	2.1			1.1	-1.1					
8	6	0.05	-0-	-0-	0.01	-0-	4.4			4.3	-0.7	2.3			3.2	0.4
9	1	0.05	-0-	-0-	-0-	10^{-5}	1.9									
10	6	0.05	-0-	-0-	-0-	10^{-5}	1.9					0.0				
11	1	0.05	0.05	-0-	-0-	10^{-5}	1.1	-0.2								
12	6	0.05	0.05	-0-	-0-	10^{-5}	1.2	-0.5				0.1	-0.3			
13	1	0.05	-0-	0.05	-0-	10^{-5}	2.0		0.5							
14	6	0.05	-0-	0.05	-0-	10^{-5}	1.9		0.5			-0.1		0.0		
15	1	0.05	-0-	-0-	0.01	10^{-5}	1.5			1.2						
16	6	0.05	-0-	-0-	0.01	10^{-5}	1.7			3.3		0.2			2.1	
17	1	0.05	-0-	-0-	-0-	-0-	1.5									
18	6	0.05	-0-	-0-	-0-	-0-	1.5					0.0				
19	1	0.05	0.05	-0-	-0-	-0-	0.8	-0.2								
20	6	0.05	0.05	-0-	-0-	-0-	0.8	-0.3				0.0	-0.1			
21	1	0.05	-0-	0.05	-0-	-0-	1.4		0.5							
22	6	0.05	-0-	0.05	-0-	-0-	1.5		0.5			0.1		0.0		
23	1	0.05	-0-	-0-	0.01	-0-	1.4			0.8						
24	6	0.05	-0-	-0-	0.01	-0-	1.5			2.3		0.1			1.5	

Appendix Table 3. Conditions, Treatments and Results of Experiment 6-202. The pH was 5.0 ± 0.2 and the temperature was 24 - 25°C. Initial Mn and Na content of the root material was < 0.1 and 0.4 meq/kg respectively.

Trmt. No.	Time	Treatment Solution Composition				Uptake		Absorption Rate	
		$MnCl_2$	NaCl	Arsenate	Azide	Mn	Na	Mn	Na
	hour	meq/l	M	M	M	meq/kg		meq/kg/5hr	
9	1	0.05				2.0	-0.1		
10	6	0.05				5.3	-0.1	3.3	
11	1	0.05	10^{-4}			1.6	2.2		
12	6	0.05	10^{-4}			3.4	10.0	1.8	7.8
13	1	0.05		10^{-4}		1.5	0.6		
14	6	0.05		10^{-4}		2.5	1.3	1.0	0.7
15	1	0.05			10^{-4}	1.6	0.5		
16	6	0.05			10^{-4}	2.0	0.2	0.4	-0.3

Appendix Table 4. Conditions, Treatments and Results of Experiment 5-311. The pH treatments used were 3, 4, 5, 6 and 7. The range of variation of these values were 3.0 ± 0, 4.0 ± 0.5, 5.0 - 5.2, 5.9 - 6.4 and 6.7 - 7.2 respectively. The temperature was 25 ± 0.5°C. Initial Mn and Ca content of the root material was < 0.1 and 2.4 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	pH	Trmt. Soln. Composition	Uptake	Absorption Rate
			Mn	Mn	Mn
	hour		meq/liter	meq/kg	meq/kg/5hr
1	1	3	0.05	-0-	
2	6	3	0.05	-0-	0.0
7	1	4	0.05	0.5	
8	6	4	0.05	0.7	0.2
13	1	5	0.05	1.8	
14	6	5	0.05	4.9	3.1
19	1	6	0.05	3.0	
20	6	6	0.05	9.2	6.2
25	1	7	0.05	3.0	
26	6	7	0.05	8.1	5.1

Appendix Table 5. Conditions, Treatments and Results of Experiment 6-201. The pH was 4.9 - 5.15 and the temperature was 24.5 - 25°C. Initial Mn and K content of the root material was < 0.1 and 18.8 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Mn Trmt. Concentration	Mn Uptake	Mn Absorption Rate	Final K Content
	hour	meq/liter	meq/kg	meq/kg/5hr	meq / kg
1	1	0.001	0.1		16.3
2	6	0.001	0.2	0.1	17.7
3	1	0.005	0.7		16.9
4	6	0.005	1.1	0.4	17.7
5	1	0.01	1.0		17.3
6	6	0.01	2.0	1.0	18.4
7	1	0.05	2.0		17.7
8	6	0.05	4.8	2.8	18.2
9	1	0.1	2.3		17.2
10	6	0.1	6.2	3.9	18.2
11	1	0.3	3.3		17.9
12	6	0.3	10.2	6.9	18.5
13	1	0.5	3.5		17.7
14[1]	6	0.5	9.2	5.7	24.6
15	1	1.0	3.9		17.7
16	6	1.0	13.0	9.1	18.2
17	1	3.0	4.7		17.3
18	6	3.0	15.7	11.0	18.7
19	1	5.0	5.0		17.7
20	6	5.0	16.7	11.7	16.9
21	1	10	5.4		18.2
22	6	10	17.0	11.6	17.5

1/ Treatment apparently contaminated with K.

Appendix Table 6. Conditions, Treatments and Results of Experiment 4-210. The pH was 5.0 ± 0.2 and the temperature was 25 ± 0°C. Initial K and Mn content of the root material was 22.3 and < 0.1 meq/kg respectively.

Trmt. No.	Time	Trmt. Soln. Composition		Uptake		Absorption Rate	
		K	Mn	K	Mn	K	Mn
	hour	meq/liter		meq/kg		meq/kg/5hr	
1	1	5	-0-	9.1	0.0		
2	6	5	-0-	42.7	0.0	33.6	0.0
3	1	5	0.1	9.9	0.7		
4	6	5	0.1	45.7	1.9	35.8	1.2
5	1	5	0.5	9.1	1.6		
6	6	5	0.5	46.4	4.9	37.3	3.3
7	1	5	1.0	8.4	1.9		
8	6	5	1.0	42.0	6.8	33.6	4.9
9	1	5	5	9.1	2.9		
10	6	5	5	35.4	11.6	26.3	8.7
11	1	5	10	9.1	3.6		
12	6	5	10	28.9	13.9	19.8	10.3
13	1	5	25	9.1	4.4		
14	6	5	25	25.2	16.3	14.1	11.9

Appendix Table 7. Conditions, Treatments and Results of Experiment 5-22. The pH was 4.8 - 5.0 and the temperature was 25°C. Initial Mn and Mg content of the root material was < 0.1 and 10.2 meq/kg respectively. All ions were provided as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition		Uptake		Absorption Rate	
		Mn	Mg	Mn	Mg	Mn	Mg
	hour	meq/liter		meq/kg		meq/kg/5hr	
1	1	-0-	5	0.0	4.4		
2	6	-0-	5	0.0	18.9	0.0	14.5
3	1	0.001	5	0.0	4.4		
4	6	0.001	5	0.0	19.2	0.0	14.8
5	1	0.01	5	0.0	4.4		
6	6	0.01	5	0.2	18.7	0.2	14.3
7	1	0.05	5	0.1	3.7		
8	6	0.05	5	0.6	17.1	0.5	13.4
9	1	0.1	5	0.2	3.2		
10	6	0.1	5	0.9	14.9	0.7	11.7
11	1	0.5	5	0.7	1.8		
12	6	0.5	5	2.5	6.2	1.8	4.4
13	1	1.0	5	1.1	1.3		
14	6	1.0	5	3.7	3.8	2.6	2.5
15	1	5.0	5	2.5	0.3		
16	6	5.0	5	7.2	1.4	4.7	1.1

Appendix Table 8. Conditions, Treatments and Results of Experiment 5-34. The pH was 5.0 - 5.2 and the temperature was 25°C. Initial Mn, Ca and Mg content of the root material was < 0.1, 3.0 and 10.2 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	Mg	Mn	Ca	Mg	Mn	Ca	Mg
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	1.8		-1.9			
2	6	0.05	-0-	-0-	5.4		-2.3	3.6		-0.4
3	1	0.05	-0-	0.001	1.6		-1.9			
4	6	0.05	-0-	0.001	5.3		-2.1	3.7		-0.2
5	1	0.05	-0-	0.005	1.7		-1.6			
6	6	0.05	-0-	0.005	4.3		-1.6	2.6		0.0
7	1	0.05	-0-	0.01	1.5		-1.5			
8	6	0.05	-0-	0.01	4.2		-1.5	2.7		0.0
9	1	0.05	-0-	0.025	1.3		-1.0			
10	6	0.05	-0-	0.025	3.3		-0.8	2.0		0.2
11	1	0.05	-0-	0.05	1.0		-0.7			
12	6	0.05	-0-	0.05	2.7		-0.3	1.7		0.4
13	1	0.05	-0-	0.1	0.7		0.0			
14	6	0.05	-0-	0.1	2.2		0.7	1.5		0.7
15	1	0.05	0.05	-0-	1.0	-0.5	-1.9			
16	6	0.05	0.05	-0-	4.9	-0.3	-2.0	3.9	0.2	-0.1
17	1	0.05	0.05	0.001	1.0	-0.4	-2.0			
18	6	0.05	0.05	0.001	4.4	0.0	-2.1	3.4	0.4	-0.1
19	1	0.05	0.05	0.005	0.9	-0.4	-1.6			
20	6	0.05	0.05	0.005	3.3	-0.5	-1.7	2.4	-0.1	-0.1
21	1	0.05	0.05	0.01	0.9	-0.5	-1.6			
22	6	0.05	0.05	0.01	2.8	-0.4	-1.5	1.9	0.1	0.1
23	1	0.05	0.05	0.025	0.8	-0.8	-1.5			
24	6	0.05	0.05	0.025	2.0	-0.7	-0.8	1.2	0.1	0.7
25	1	0.05	0.05	0.05	0.7	-0.8	-1.4			
26	6	0.05	0.05	0.05	1.5	-0.8	-0.6	0.8	0.0	0.8
27	1	0.05	0.05	0.1	0.5	-0.9	-0.8			
28	6	0.05	0.05	0.1	1.1	-0.9	0.0	0.6	0.0	0.8

Appendix Table 9. Conditions, Treatments and Results of Experiment 5-22. The pH was 4.8 - 5.0 and the temperature was 25°C. Initial Mn and Mg content of the root material was < 0.1 and 10.2 respectively. All ions were provided as chloride salts.

Trmt. No.	Mn Pretreatment		Content After Pretreatment		Uptake[1]	Mg Uptake	Mg Absorption Rate
	Time	Conc.	Mn	Mg	Time		
	hour	meq/liter	meq/kg		hour	meq/kg	meq/kg/5hr
	1	0.01	0.9	8.9			
	1	0.1	2.5	8.5			
	1	1.0	4.0	8.5			
	1	10.0	6.1	8.2			
1	None				1	4.4	
2	None				6	18.9	14.5
19	1	0.01			1	5.8	
20	1	0.01			6	20.5	14.7
21	1	0.1			1	6.1	
22	1	0.1			6	20.2	14.1
23	1	1.0			1	6.4	
24	1	1.0			6	19.0	12.6
25	1	10.0			1	6.6	
26	1	10.0			6	18.6	12.0

1/ After the Mn pretreatment, the roots were thoroughly washed in distilled water and immersed into 5×10^{-3} N $MgCl_2$ for the time indicated.

Appendix Table 10. Conditions, Treatments and Results of Experiment 5-35. The pH was 4.9 - 5.2 and the temperature was 24.5 - 25°C. Initial Mn, Mg, and Ca content of the root material was < 0.1, 10.0 and 2.6 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Mg	Ca	Mn	Mg	Ca	Mn	Mg	Ca
	hour		meq/liter			meq/kg			meq/kg/5hr	
1	1	0.05	-0-	-0-	1.9	-1.6	-1.1			
2	6	0.05	-0-	-0-	4.8	-1.9	-1.3	2.9	-0.3	-0.2
3	1	0.05	-0-	0.01	1.7	-1.4	-0.8			
4	6	0.05	-0-	0.01	4.8	-1.6	-0.9	3.1	-0.2	-0.1
5	1	0.05	-0-	0.05	1.2	-1.4	-0.2			
6	6	0.05	-0-	0.05	4.7	-1.9	-0.2	3.5	-0.5	0.0
7	1	0.05	-0-	0.1	0.9	-1.6	0.2			
8	6	0.05	-0-	0.1	4.6	-2.0	0.4	3.7	-0.4	0.2
9	1	0.05	-0-	0.5	0.4	-1.6	0.9			
10	6	0.05	-0-	0.5	3.7	-1.6	1.0	3.3	0.0	0.1
11	1	0.05	-0-	1.0	0.4	-1.5	1.3			
12	6	0.05	-0-	1.0	3.0	-1.6	1.4	2.6	-0.1	0.1
13	1	0.05	-0-	5.0	0.1	-1.6	1.7			
14	6	0.05	-0-	5.0	1.4	-1.9	1.9	1.3	-0.3	0.2
15	1	0.05	-0-	10.0	0.1	-1.5	1.9			
16	6	0.05	-0-	10.0	0.9	-1.6	2.1	0.9	-0.1	0.2
17	1	0.05	0.05	-0-	1.1	-0.8	-1.2			
18	6	0.05	0.05	-0-	2.4	-0.7	-1.3	1.3	0.1	-0.1
19	1	0.05	0.05	0.01	1.0	-0.8	-0.9			
20	6	0.05	0.05	0.01	1.8	-0.7	-1.0	0.8	0.1	-0.1
21	1	0.05	0.05	0.05	0.8	-0.8	-0.4			
22	6	0.05	0.05	0.05	1.4	-0.1	-0.5	0.6	0.7	-0.1
23	1	0.05	0.05	0.1	0.7	-0.8	0.0			
24	6	0.05	0.05	0.1	1.2	-0.4	-0.1	0.5	0.4	-0.1
25	1	0.05	0.05	0.5	0.3	-1.1	0.9			
26	6	0.05	0.05	0.5	1.1	-0.4	0.8	0.8	0.7	-0.1
27	1	0.05	0.05	1.0	0.2	-1.1	1.1			
28	6	0.05	0.05	1.0	1.1	-0.6	1.1	0.9	0.5	0.0

Appendix Table 11. Conditions, Treatments and Results of Experiment 5-33. The pH was 4.95 - 5.15 and the temperature was 24.5 - 25.5°C. Initial Mn, Ca and Mg content of the root material was < 0.1, 2.7 and 10.4 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	Mg	Mn	Ca	Mg	Mn	Ca	Mg
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.5	-0-	-0-	3.5		-1.2			
2	6	0.5	-0-	-0-	13.8		-1.7	10.3		-0.5
3	1	0.5	-0-	0.001	3.5		-1.4			
4	6	0.5	-0-	0.001	14.1		-1.7	10.6		-0.3
5	1	0.5	-0-	0.01	3.3		-1.2			
6	6	0.5	-0-	0.01	13.5		-1.2	10.2		0.0
7	1	0.5	-0-	0.05	3.0		-1.0			
8	6	0.5	-0-	0.05	10.5		-1.0	7.5		0.0
9	1	0.5	-0-	0.1	2.8		-1.0			
10	6	0.5	-0-	0.1	8.3		-0.5	5.5		0.5
11	1	0.5	-0-	0.5	2.1		-0.3			
12	6	0.5	-0-	0.5	6.1		1.1	4.0		1.4
13	1	0.5	0.5	-0-	2.1	0.2	-1.5			
14	6	0.5	0.5	-0-	12.6	0.2	-1.7	10.5	0.0	-0.2
15	1	0.5	0.5	0.001	2.2	0.2	-1.6			
16	6	0.5	0.5	0.001	12.5	0.3	-1.7	10.3	0.1	-0.1
17	1	0.5	0.5	0.01	2.1	0.3	-1.5			
18	6	0.5	0.5	0.01	11.2	0.4	-1.4	9.1	0.1	0.1
19	1	0.5	0.5	0.05	1.9	0.2	-1.2			
20	6	0.5	0.5	0.05	7.6	0.3	-0.5	5.7	0.1	0.7
21	1	0.5	0.5	0.1	1.5	0.1	-1.2			
22	6	0.5	0.5	0.1	5.1	0.2	-0.1	3.6	0.1	1.1
23	1	0.5	0.5	0.5	1.2	0.0	-0.5			
24	6	0.5	0.5	0.5	2.5	-0.1	1.1	1.3	-0.1	1.6

Appendix Table 12. Conditions, Treatments and Results of Experiment 4-28. The pH was 4.9 - 5.2 and the temperature was 24.5°C. Initial K, Mn, Ca and Mg content of the root material was 19.8, < 0.1, 2.9 and 9.9 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		K	Mn	Ca	Mg	K	Mn	Ca	Mg	K	Mn	Ca	Mg
	hour	meq/liter				meq/kg				meq/kg/5hr			
3	1	5	-0-	-0-	-0-	9.1							
4	6	5	-0-	-0-	-0-	29.2				20.1			
5	1	5	5	-0-	-0-	9.4	3.1						
6	6	5	5	-0-	-0-	30.3	12.4			20.9	9.3		
7	1	5	10	-0-	-0-	9.4	3.5						
8	6	5	10	-0-	-0-	25.9	13.4			16.5	9.9		
9	1	5	15	-0-	-0-	9.4	1.8						
10	6	5	15	-0-	-0-	16.0	13.9			6.6	12.1		
11	1	5	-0-	5	-0-	11.3		1.1					
12	6	5	-0-	5	-0-	53.3		1.0		42.0		-0.1	
13	1	5	-0-	10	-0-	11.6		1.3					
14	6	5	-0-	10	-0-	51.1		1.3		39.5		0.0	
15	1	5	-0-	15	-0-	12.0		1.7					
16	6	5	-0-	15	-0-	51.5		1.5		39.5		-0.2	

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Appendix Table 12. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		K	Mn	Ca	Mg	K	Mn	Ca	Mg	K	Mn	Ca	Mg
		meq/liter				meq/kg				meq/kg/5hr			
17	1	5	-0-	-0-	5	12.4			1.4				
18	6	5	-0-	-0-	5	48.9			5.9	36.5			4.5
19	1	5	-0-	-0-	10	11.6			2.3				
20	6	5	-0-	-0-	10	48.5			7.1	36.9			4.8
21	1	5	-0-	-0-	15	12.7			2.4				
22	6	5	-0-	-0-	15	50.4			8.1	37.7			5.7
23	1	5	-0-	5	5	10.9		0.4	-0.1				
24	6	5	-0-	5	5	53.3		0.2	0.4	42.4		-0.2	0.5
25	1	5	5	-0-	5	14.2	1.8		0.0				
26	6	5	5	-0-	5	47.4	5.9		0.2	33.2	4.1		0.2
27	1	5	5	5	-0-	10.5	1.7	0.2					
28	6	5	5	5	-0-	32.8	9.5	0.2		22.3	7.8	0.0	
29	1	5	5	5	5	12.7	0.9	0.0	-0.1				
30	6	5	5	5	5	55.5	1.7	-0.2	0.4	42.8	0.8	-0.2	0.5

Appendix Table 13. Conditions, Treatments and Results of Experiment 5-315. The pH treatments used were 4, 5, 6 and 7. The range of variation of these values was 4.0 - 4.1, 5.0 - 5.1, 6.0 - 6.2 and 6.6 - 7.5, respectively. The temperature was 25°C. Initial Mn, Ca and Mg content of the root material was < 0.1, 2.3 and 9.9 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	pH	Trmt. Soln. Composition			Uptake			Absorption Rate		
			Mn	Ca	Mg	Mn	Ca	Mg	Mn	Ca	Mg
	hour		meq/liter			meq/kg			meq/kg/5hr		
1	1	4	0.05	-0-	-0-	0.4					
2	6	4	0.05	-0-	-0-	0.6			0.2		
3	1	5	0.05	-0-	-0-	1.8					
4	6	5	0.05	-0-	-0-	4.4			2.6		
5	1	6	0.05	-0-	-0-	2.9					
6	6	6	0.05	-0-	-0-	9.9			7.0		
7	1	7	0.05	-0-	-0-	2.7					
8	6	7	0.05	-0-	-0-	7.2			4.5		
9	1	4	0.05	0.05	-0-	0.2	-0.8				
10	6	4	0.05	0.05	-0-	0.4	-1.1		0.2	-0.3	
11	1	5	0.05	0.05	-0-	0.9	0.0				
12	6	5	0.05	0.05	-0-	3.4	0.1		2.5	0.1	
13	1	6	0.05	0.05	-0-	1.9	0.5				
14	6	6	0.05	0.05	-0-	8.9	0.8		7.0	0.3	
15	1	7	0.05	0.05	-0-	1.9	0.5				
16	6	7	0.05	0.05	-0-	6.9	1.2		5.0	0.7	

Continued on next page

Appendix Table 13. (continued)

Trmt. No.	Time	pH	Trmt. Soln. Composition			Uptake			Absorption Rate		
			Mn	Ca	Mg	Mn	Ca	Mg	Mn	Ca	Mg
	hour		meq/liter			meq/kg			meq/kg/5hr		
17	1	4	0.05	-0-	0.05	0.4		-2.6			
18	6	4	0.05	-0-	0.05	0.6		-4.8	0.2		-2.2
19	1	5	0.05	-0-	0.05	1.1		-1.0			
20	6	5	0.05	-0-	0.05	2.7		-1.0	1.6		0.0
21	1	6	0.05	-0-	0.05	1.9		-0.5			
22	6	6	0.05	-0-	0.05	4.5		0.4	2.6		0.9
23	1	7	0.05	-0-	0.05	2.0		-0.7			
24	6	7	0.05	-0-	0.05	4.9		0.7	2.9		1.4
25	1	4	0.05	0.05	0.05	0.3	-0.8	-2.4			
26	6	4	0.05	0.05	0.05	0.4	-1.1	-3.8	0.1	-0.3	-1.4
27	1	5	0.05	0.05	0.05	0.7	-0.2	-1.5			
28	6	5	0.05	0.05	0.05	1.5	-0.2	-1.1	0.8	0.0	0.4
29	1	6	0.05	0.05	0.05	1.2	0.1	-1.1			
30	6	6	0.05	0.05	0.05	3.0	0.2	-0.1	1.8	0.1	1.0
31	1	7	0.05	0.05	0.05	1.5	0.2	-0.9			
32	6	7	0.05	0.05	0.05	3.8	0.5	0.6	2.3	0.3	1.5

Appendix Table 14. Conditions, Treatments and Results of Experiment 5-316. The pH was 4.9 - 5.3 and the temperature was 24 - 32°C. Initial Mn, Ca and Mg content of the root material was < 0.1, 2.7 and 10.8 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition					Uptake			Absorption Rate		
		Mn	Ca	Mg	Sr	Ba	Mn	Ca	Mg	Mn	Ca	Mg
	hour	meq/liter					meq/kg			meq/kg/5hr		
1	1	0.05	-0-	0.05	-0-	-0-	1.4		-0.7			
2	6	0.05	-0-	0.05	-0-	-0-	3.8		0.3	2.4		1.0
3	1	0.05	0.05	-0-	-0-	-0-	1.1	-0.1				
4	6	0.05	0.05	-0-	-0-	-0-	6.2	0.1		5.1	0.2	
5	1	0.05	-0-	-0-	0.05	-0-	1.5					
6	6	0.05	-0-	-0-	0.05	-0-	5.3			3.8		
7	1	0.05	-0-	-0-	-0-	0.05	1.4					
8	6	0.05	-0-	-0-	-0-	0.05	4.8			3.4		
9	1	0.05	0.05	0.05	-0-	-0-	1.0	-0.2	-0.7			
10	6	0.05	0.05	0.05	-0-	-0-	2.2	-0.1	0.7	1.2	0.1	1.4
11	1	0.05	-0-	0.05	0.05	-0-	1.1		-0.7			
12	6	0.05	-0-	0.05	0.05	-0-	2.7		0.7	1.6		1.4
13	1	0.05	-0-	0.05	-0-	0.05	1.0		-1.0			
14	6	0.05	-0-	0.05	-0-	0.05	2.6		0.1	1.6		1.1
15	1	0.05	0.05	-0-	0.05	-0-	1.2	-0.2				
16	6	0.05	0.05	-0-	0.05	-0-	5.5	-0.2		4.3	0.0	
17	1	0.05	0.05	-0-	-0-	0.05	1.1	-0.3				
18	6	0.05	0.05	-0-	-0-	0.05	5.0	-0.2		3.9	0.1	
19	1	0.05	-0-	-0-	0.05	0.05	1.1					
20	6	0.05	-0-	-0-	0.05	0.05	4.2			3.1		
21	1	0.05	-0-	-0-	-0-	-0-	2.4	-1.1	-1.4			
22	6	0.05	-0-	-0-	-0-	-0-	6.2	-1.2	-1.9	3.8	-0.1	-0.5

Appendix Table 15. Conditions, Treatments and Results of Experiment 5-312. The pH was 4.9 - 5.2 and the temperature was 25°C. Initial Mn and Ca content of the root material was < 0.1 and 2.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake		Absorption Rate	
		Mn	Ca	Ba	Mn	Ca	Mn	Ca
	hour	meq/liter			meq/kg		meq/kg/5hr	
1	1	0.05	-0-	-0-	2.1			
2	6	0.05	-0-	-0-	5.2		3.1	
3	1	0.05	-0-	0.005	2.0			
4	6	0.05	-0-	0.005	5.1		3.1	
5	1	0.05	-0-	0.05	1.2			
6	6	0.05	-0-	0.05	3.6		2.4	
7	1	0.05	-0-	0.1	0.9			
8	6	0.05	-0-	0.1	3.1		2.2	
9	1	0.05	-0-	0.5	0.4			
10	6	0.05	-0-	0.5	1.6		1.2	
11	1	0.05	-0-	1.0	0.2			
12	6	0.05	-0-	1.0	1.1		0.9	
13	1	0.05	0.5	-0-	0.4	1.7		
14	6	0.05	0.5	-0-	3.5	2.0	3.1	0.3
15	1	0.05	0.5	0.005	0.5	1.6		
16	6	0.05	0.5	0.005	3.4	1.9	2.9	0.3
17	1	0.05	0.5	0.05	0.4	1.5		
18	6	0.05	0.5	0.05	3.1	1.6	2.7	0.1
19	1	0.05	0.5	0.1	0.4	1.4		
20	6	0.05	0.5	0.1	3.0	1.4	2.6	0.0
21	1	0.05	0.5	0.5	0.3	0.6		
22	6	0.05	0.5	0.5	2.0	0.7	1.7	0.1
23	1	0.05	0.5	1.0	0.3	0.2		
24	6	0.05	0.5	1.0	1.7	0.2	1.4	0.0

Appendix Table 16. Conditions, Treatments and Results of Experiment 5-318. The pH was 4.9 - 5.3 and the temperature was 24 - 25°C. Initial Mn, Ca, Mg and Fe content of the root material was < 0.1, 2.4, 9.2 and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Fe++	Mn	Ca	Mg	Fe	Mn	Ca	Mg	Fe
	hour	meq/liter				meq/kg				meq/kg/5hr			
1	1	0.05	-0-	-0-	-0-	1.9			-0.1				
2	6	0.05	-0-	-0-	-0-	4.7			-0.1	2.8			0.0
3	1	0.05	-0-	-0-	0.001	2.0			0.2				
4	6	0.05	-0-	-0-	0.001	4.3			0.5	2.3			0.3
5	1	0.05	-0-	-0-	0.005	1.8			0.9				
6	6	0.05	-0-	-0-	0.005	4.0			2.3	2.2			1.4
7	1	0.05	-0-	-0-	0.01	1.6			1.3				
8	6	0.05	-0-	-0-	0.01	3.8			3.5	2.2			2.2
9	1	0.05	-0-	-0-	0.05	1.0			2.5				
10	6	0.05	-0-	-0-	0.05	2.9			8.1	1.9			5.6
11	1	0.05	-0-	-0-	0.10	0.8			3.4				
12	6	0.05	-0-	-0-	0.10	2.5			11.0	1.7			7.6
13	1	0.05	0.05	-0-	-0-	1.2	0.1		0.0				
14	6	0.05	0.05	-0-	-0-	4.4	0.0		0.0	3.2	-0.1		0.0
15	1	0.05	0.05	-0-	0.001	1.1	0.0		0.4				
16	6	0.05	0.05	-0-	0.001	3.3	-0.2		0.5	2.2	-0.2		0.1
17	1	0.05	0.05	-0-	0.005	1.0	-0.1		0.8				
18	6	0.05	0.05	-0-	0.005	2.4	-0.2		2.1	1.4	-0.1		1.3

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Appendix Table 16. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Fe++	Mn	Ca	Mg	Fe	Mn	Ca	Mg	Fe
	hour	meq/liter				meq/kg				meq/kg/5hr			
19	1	0.05	0.05	-0-	0.01	0.9	-0.2		1.1				
20	6	0.05	0.05	-0-	0.01	2.1	-0.2		3.4	1.2	0.0		2.3
21	1	0.05	0.05	-0-	0.05	0.7	-0.3		2.3				
22	6	0.05	0.05	-0-	0.05	1.5	-0.4		8.5	0.8	-0.1		6.2
23	1	0.05	0.05	-0-	0.10	0.5	-0.4		3.2				
24	6	0.05	0.05	-0-	0.10	1.1	-0.5		10.9	0.6	-0.1		7.7
25	1	0.05	-0-	0.05	-0-	1.4		-0.4	-0.1				
26	6	0.05	-0-	0.05	-0-	2.4		-0.6	0.0	1.0		-0.2	0.1
27	1	0.05	-0-	0.05	0.001	1.2		-0.7	0.4				
28	6	0.05	-0-	0.05	0.001	2.2		-0.6	0.5	1.0		0.1	0.1
29	1	0.05	-0-	0.05	0.005	0.9		-0.6	0.6				
30	6	0.05	-0-	0.05	0.005	2.1		-0.6	2.0	1.2		0.0	1.4
31	1	0.05	-0-	0.05	0.01	1.0		-0.7	0.9				
32	6	0.05	-0-	0.05	0.01	2.2		-0.7	3.1	1.2		0.0	2.2
33	1	0.05	-0-	0.05	0.05	0.8		-0.7	2.3				
34	6	0.05	-0-	0.05	0.05	1.7		-1.1	6.2	0.9		-0.4	3.9
35	1	0.05	-0-	0.05	0.10	0.6		-0.7	2.9				
36	6	0.05	-0-	0.05	0.10	1.5		-1.3	8.6	0.9		-0.6	5.7

Appendix Table 17. Conditions, Treatments and Results of Experiment 6-101. The pH was 5.0 - 5.2 and the temperature was 24 - 25°C. Initial Mn, Mg, and Zn content of the root material was < 0.1, 10.0, and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake			Absorption Rate		
		Mn	Ca	Mg	Zn	Mn	Mg	Zn	Mn	Mg	Zn
	hour	meq/liter				meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	-0-	1.7		0.0			
2	6	0.05	-0-	-0-	-0-	5.3		0.0	3.6		0.0
3	1	0.05	-0-	-0-	0.001	1.6		0.1			
4	6	0.05	-0-	-0-	0.001	1J		0.1	1J		0.0
5	1	0.05	-0-	-0-	0.005	1.5		0.2			
6	6	0.05	-0-	-0-	0.005	3.8		0.7	2.3		0.5
7	1	0.05	-0-	-0-	0.01	1.4		0.4			
8	6	0.05	-0-	-0-	0.01	3.4		1.1	2.0		0.7
9	1	0.05	-0-	-0-	0.05	0.9		1.2			
10	6	0.05	-0-	-0-	0.05	1.8		2.4	0.9		1.2
11	1	0.05	-0-	-0-	0.1	1.1		1.6			
12	6	0.05	-0-	-0-	0.1	1.2		2.9	0.1		1.3
13	1	0.05	0.05	-0-	-0-	1.0		0.0			
14	6	0.05	0.05	-0-	-0-	4.6		0.0	3.6		0.0
15	1	0.05	0.05	-0-	0.001	1.0		0.0			
16	6	0.05	0.05	-0-	0.001	4.2		0.2	3.2		0.2
17	1	0.05	0.05	-0-	0.005	0.9		0.2			
18	6	0.05	0.05	-0-	0.005	3.3		0.7	2.4		0.5
19	1	0.05	0.05	-0-	0.01	0.8		0.3			
20	6	0.05	0.05	-0-	0.01	2.5		1.1	1.7		0.8

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Appendix Table 17. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake			Absorption Rate		
		Mn	Ca	Mg	Zn	Mn	Mg	Zn	Mn	Mg	Zn
	hour	meq/liter				meq/kg			meq/kg/5hr		
21	1	0.05	0.05	-0-	0.05	0.6		0.8			
22	6	0.05	0.05	-0-	0.05	1.2		2.2	0.6		1.4
23	1	0.05	0.05	-0-	0.1	0.4		1.3			
24	6	0.05	0.05	-0-	0.1	0.8		2.8	0.4		1.5
25	1	0.05	-0-	0.05	-0-	0.9	-1.2	0.0			
26	6	0.05	-0-	0.05	-0-	2.9	-1.1	0.0	2.0	0.1	0.0
27	1	0.05	-0-	0.05	0.001	1.1	-1.3	0.1			
28	6	0.05	-0-	0.05	0.001	2.7	-0.8	0.1	1.6	0.5	0.0
29	1	0.05	-0-	0.05	0.005	1.1	-1.0	0.2			
30	6	0.05	-0-	0.05	0.005	2.5	-1.2	0.4	1.4	-0.2	0.2
31	1	0.05	-0-	0.05	0.01	1.0	-1.3	0.3			
32	6	0.05	-0-	0.05	0.01	2.3	-1.5	0.6	1.3	-0.2	0.3
33	1	0.05	-0-	0.05	0.05	0.7	-1.3	1.0			
34	6	0.05	-0-	0.05	0.05	1.6	-2.4	2.1	0.9	-1.1	1.1
35	1	0.05	-0-	0.05	0.1	0.6	-1.5	1.5			
36	6	0.05	-0-	0.05	0.1	1.1	-3.1	2.8	0.5	-1.6	1.3
37	1	-0-	-0-	-0-	0.05			1.6			
38	6	-0-	-0-	-0-	0.05			2.4			0.8

1/ Root sample was lost during the chemical analysis

Appendix Table 18. Conditions, Treatments and Results of Experiment 6-105. The pH was 4.9 - 5.2 and the temperature was 25 ± 0.5°C. Initial Mn, Ca, Mg, Cu and K content of the root material was < 0.1, 2.6, 11.0, < 0.1 and 20.4 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake					Absorption Rate				
		Mn	Ca	Mg	Cu	Mn	Ca	Mg	Cu	K	Mn	Ca	Mg	Cu	K
	hour	meq/liter				meq/kg					meq/kg/5hr				
1	1	0.05	-0-	-0-	-0-	1.7			0.1	-1.8					
2	6	0.05	-0-	-0-	-0-	4.5			0.2	-1.6	2.8			0.1	0.2
3	1	0.05	-0-	-0-	0.001	2.0			0.3	-2.5					
4	6	0.05	-0-	-0-	0.001	4.4			0.4	-3.6	2.4			0.1	-1.1
5	1	0.05	-0-	-0-	0.005	2.2			0.8	-3.0					
6	6	0.05	-0-	-0-	0.005	2.8			1.1	-9.1	0.6			0.3	-6.1
7	1	0.05	-0-	-0-	0.01	2.2			1.2	-4.1					
8	6	0.05	-0-	-0-	0.01	1.9			1.6	-11.8	-0.3			0.4	-7.7
9	1	0.05	-0-	-0-	0.05	1.2			2.9	-6.9					
10	6	0.05	-0-	-0-	0.05	0.8			3.7	-17.5	-0.4			0.8	-10.6
11	1	0.05	-0-	-0-	0.1	0.9			3.9	-8.0					
12	6	0.05	-0-	-0-	0.1	0.5			4.5	-18.2	-0.4			0.6	-10.2
13	1	0.05	0.05	-0-	-0-	1.1	-0.2		0.1	-0.7					
14	6	0.05	0.05	-0-	-0-	3.7	-0.1		0.2	0.4	2.6	0.1		0.1	1.1
15	1	0.05	0.05	-0-	0.001	1.2	0.0		0.2	-1.0					
16	6	0.05	0.05	-0-	0.001	3.3	0.1		0.4	-0.7	2.1	0.1		0.2	0.3
17	1	0.05	0.05	-0-	0.005	1.1	0.0		0.6	-0.3					
18	6	0.05	0.05	-0-	0.005	2.1	0.1		1.0	-1.8	1.0	0.1		0.4	-1.5

Continued on next page

Appendix Table 18. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake					Absorption Rate				
		Mn	Ca	Mg	Cu	Mn	Ca	Mg	Cu	K	Mn	Ca	Mg	Cu	K
	hour		meq/liter				meq/kg					meq/kg/5hr			
19	1	0.05	0.05	-0-	0.01	1.1	0.0		1.0	-1.6					
20	6	0.05	0.05	-0-	0.01	1.5	-0.2		1.4	-5.2	0.4	-0.2		0.4	-3.6
21	1	0.05	0.05	-0-	0.05	0.7	-0.4		2.4	-4.0					
22	6	0.05	0.05	-0-	0.05	0.7	-1.2		3.0	-14.6	0.0	-0.8		0.6	-10.6
23	1	0.05	0.05	-0-	0.1	0.5	-0.5		3.2	-4.9					
24	6	0.05	0.05	-0-	0.1	0.5	-1.7		4.1	-16.2	0.0	-1.2		0.9	-11.3
25	1	0.05	-0-	0.05	-0-	1.4		-1.1	0.1	-1.6					
26	6	0.05	-0-	0.05	-0-	3.4		-0.9	0.2	-0.5	2.0		0.2	0.1	1.1
27	1	0.05	-0-	0.05	0.001	1.4		-0.7	0.2	-1.0					
28	6	0.05	-0-	0.05	0.001	3.4		-0.9	0.4	-1.9	2.0		-0.2	0.2	-0.9
29	1	0.05	-0-	0.05	0.005	1.6		-1.2	0.7	-1.2					
30	6	0.05	-0-	0.05	0.005	2.5		-1.7	1.0	-8.0	0.9		-0.5	0.3	-6.8
31	1	0.05	-0-	0.05	0.01	1.5		-1.4	1.0	-1.8					
32	6	0.05	-0-	0.05	0.01	1.7		-3.0	1.5	-11.3	0.2		-1.6	0.5	-9.5
33	1	0.05	-0-	0.05	0.05	1.0		-1.8	2.6	-6.1					
34	6	0.05	-0-	0.05	0.05	0.7		-7.6	3.2	-17.3	-0.3		-5.8	0.6	-11.2
35	1	0.05	-0-	0.05	0.1	0.7		-2.2	3.6	-8.0					
36	6	0.05	-0-	0.05	0.1	0.5		-8.4	4.4	-18.4	-0.2		-6.2	0.8	-10.4
37	1	-0-	-0-	-0-	0.05		-1.1	-2.5	3.6	-8.2					
38	6	-0-	-0-	-0-	0.05		-2.1	-8.4	3.7	-18.0		-1.0	-5.9	0.1	-9.8

Appendix Table 19. Conditions, Treatments and Results of Experiment 5-313. The pH was 4.9 - 5.2 except the 0.5 & 1.0 meq per liter Al treatments which were 4.7 - 4.9 & 4.65 - 4.7 respectively. The temperature was 24 - 24.5°C. Initial Mn and Ca content of the root material was < 0.1 and 2.8 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake		Absorption Rate	
		Mn	Ca	Al	Mn	Ca	Mn	Ca
	hour	meq/liter			meq/kg		meq/kg/5hr	
1	1	0.05	-0-	-0-	1.8			
2	6	0.05	-0-	-0-	4.2		2.4	
3	1	0.05	-0-	0.005	1.3			
4	6	0.05	-0-	0.005	3.0		1.7	
5	1	0.05	-0-	0.05	0.4			
6	6	0.05	-0-	0.05	0.9		0.5	
7	1	0.05	-0-	0.1	0.3			
8	6	0.05	-0-	0.1	0.6		0.3	
9	1	0.05	-0-	0.5	0.1			
10	6	0.05	-0-	0.5	0.2		0.1	
11	1	0.05	-0-	1.0	0.1			
12	6	0.05	-0-	1.0	0.2		0.1	
13	1	0.05	0.5	-0-	0.4	1.0		
14	6	0.05	0.5	-0-	2.7	1.0	2.3	0.0
15	1	0.05	0.5	0.005	0.3	0.7		
16	6	0.05	0.5	0.005	0.5	0.6	0.2	-0.1
17	1	0.05	0.5	0.05	0.2	0.0		
18	6	0.05	0.5	0.05	0.2	-0.3	0.0	-0.3
19	1	0.05	0.5	0.1	0.1	-0.3		
20	6	0.05	0.5	0.1	0.2	-0.5	0.1	-0.2
21	1	0.05	0.5	0.5	0.1	-0.7		
22	6	0.05	0.5	0.5	0.1	-0.8	0.0	-0.1
23	1	0.05	0.5	1.0	0.1	-0.7		
24	6	0.05	0.5	1.0	0.1	-1.1	0.0	-0.4

Appendix Table 20. Conditions, Treatments and Results of Experiment 6-103. The pH was 5.0 ± 0.15 and the temperature was 25 ± 0.5°C. Initial Mn, Mg, Al, and K content of the root material was < 0.1, 11.5, < 0.1 and 23.2 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake				Absorption Rate			
		Mn	Mg	Al	Mn	Mg	Al	K	Mn	Mg	Al	K
	hour	meq/liter			meq/kg				meq/kg/5hr			
1	1	0.05	-0-	-0-	1.7		0.0	-2.4				
2	6	0.05	-0-	-0-	3.8		0.0	-2.4	2.1		0.0	0.0
3	1	0.05	-0-	0.001	1.6		0.0					
4	6	0.05	-0-	0.001	3.1		1.0		1.5		1.0	
5	1	0.05	-0-	0.005	1.2		1.0					
6	6	0.05	-0-	0.005	3.0		1.5		1.8		0.5	
7	1	0.05	-0-	0.01	0.8		2.0					
8	6	0.05	-0-	0.01	2.7		3.5		1.9		1.5	
9	1	0.05	-0-	0.05	0.3		4.0					
10	6	0.05	-0-	0.05	0.9		7.5		0.6		3.5	
11	1	0.05	-0-	0.1	0.2		4.5	-1.3				
12	6	0.05	-0-	0.1	0.5		9.0	-4.2	0.3		4.5	-2.9
13	1	0.05	0.05	-0-	1.1	-0.6	0.0					
14	6	0.05	0.05	-0-	2.4	-1.0	0.0		1.3	-0.4	0.0	
15	1	0.05	0.05	0.001	1.1	-0.6	0.5					
16	6	0.05	0.05	0.001	2.3	-1.2	1.5		1.2	-0.6	1.0	
17	1	0.05	0.05	0.005	0.8	-0.9	1.5					
18	6	0.05	0.05	0.005	2.5	-1.6	2.0		1.7	-0.7	0.5	
19	1	0.05	0.05	0.01	0.6	-0.7	1.0					
20	6	0.05	0.05	0.01	2.0	-1.4	2.5		1.4	-0.7	1.5	
21	1	0.05	0.05	0.05	0.3	-1.3	4.0					
22	6	0.05	0.05	0.05	0.7	-2.1	6.5		0.4	-0.8	2.5	
23	1	0.05	0.05	0.1	0.2	-1.4	4.0					
24	6	0.05	0.05	0.1	0.4	-1.9	7.5		0.2	-0.5	3.5	

Appendix Table 21. Conditions, Treatments and Results of Experiment 5-317. The pH was 4.9 - 5.3 and the temperature was 24 - 25°C. Initial Mn and Ca content of the root material was < 0.1 and 2.7 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake		Absorption Rate	
		Mn	Ca	La	Mn	Ca	Mn	Ca
	hour	meq/liter			meq/kg		meq/kg/5hr	
1	1	0.05	-0-	-0-	1.8			
2	6	0.05	-0-	-0-	4.6		2.8	
3	1	0.05	-0-	0.005	0.6			
4	6	0.05	-0-	0.005	1.1		0.5	
5	1	0.05	-0-	0.05	0.2			
6	6	0.05	-0-	0.05	0.4		0.2	
7	1	0.05	-0-	0.1	0.2			
8	6	0.05	-0-	0.1	0.3		0.1	
9	1	0.05	-0-	0.5	0.0			
10	6	0.05	-0-	0.5	0.1		0.1	
11	1	0.05	-0-	1.0	0.0			
12	6	0.05	-0-	1.0	0.1		0.1	
13	1	0.05	0.5	-0-	0.4	1.1		
14	6	0.05	0.5	-0-	3.3	1.3	2.9	0.2
15	1	0.05	0.5	0.005	0.3	0.6		
16	6	0.05	0.5	0.005	0.4	0.6	0.2	0.0
17	1	0.05	0.5	0.05	0.1	-0.2		
18	6	0.05	0.5	0.05	0.3	-0.1	0.2	0.1
19	1	0.05	0.5	0.1	0.0	-0.4		
20	6	0.05	0.5	0.1	0.2	-0.3	0.2	0.1
21	1	0.05	0.5	0.5	0.0	-0.7		
22	6	0.05	0.5	0.5	0.2	-0.7	0.2	0.0
23	1	0.05	0.5	1.0	0.0	-0.8		
24	6	0.05	0.5	1.0	0.0	-0.9	0.0	-0.1

Appendix Table 22. Conditions, Treatments and Results of Experiment 6-102. The pH was 4.9 - 5.2 and the temperature was 24 - 25°C. Initial Mn, Mg and K content of the root material was < 0.1, 9.8 and 18.6 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Mg	La	Mn	Mg	K	Mn	Mg	K
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	2.0		-1.8			
2	6	0.05	-0-	-0-	4.2		-1.1	2.2		0.7
3	1	0.05	-0-	0.001	1.7					
4	6	0.05	-0-	0.001	2.2			0.5		
5	1	0.05	-0-	0.005	0.8					
6	6	0.05	-0-	0.005	1.0			0.2		
7	1	0.05	-0-	0.01	0.4					
8	6	0.05	-0-	0.01	0.7			0.3		
9	1	0.05	-0-	0.05	0.2					
10	6	0.05	-0-	0.05	0.3			0.1		
11	1	0.05	-0-	0.1	0.1		-1.4			
12	6	0.05	-0-	0.1	0.3		-1.8	0.2		-0.4
13	1	0.05	0.05	-0-	1.2	-1.2				
14	6	0.05	0.05	-0-	2.5	-1.2		1.3	0.0	
15	1	0.05	0.05	0.001	1.1	-1.1				
16	6	0.05	0.05	0.001	1.5	-1.2		0.4	-0.1	
17	1	0.05	0.05	0.005	0.6	-1.3				
18	6	0.05	0.05	0.005	0.8	-1.8		0.2	-0.5	
19	1	0.05	0.05	0.01	0.4	-1.8				
20	6	0.05	0.05	0.01	0.6	-2.3		0.2	-0.5	
21	1	0.05	0.05	0.05	0.1	-1.8				
22	6	0.05	0.05	0.05	0.3	-2.3		0.2	-0.5	
23	1	0.05	0.05	0.1	0.1	-1.9				
24	6	0.05	0.05	0.1	0.2	-2.3		0.1	-0.4	

Appendix Table 23. Conditions, Treatments and Results of Experiment 6-110. The pH was 4.9 - 5.15 and the temperature was 24.5 - 25°C. Initial Mn and K content of the root material was < 0.1 and 18.3 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake		Absorption Rate	
		Mn	K	La	Mn	K	Mn	K
	hour	meq/liter			meq/kg		meq/kg/5hr	
7	1	0.05	-0-	-0-	2.0	-1.3		
8	6	0.05	-0-	-0-	4.8	-0.7	2.8	0.6
23	1	0.05	-0-	0.05	0.1	-1.0		
24	6	0.05	-0-	0.05	0.3	-1.0	0.2	0.0
25	1	0.05	0.5	-0-	1.5	3.2		
26	6	0.05	0.5	-0-	2.7	20.0	1.2	16.8
27	1	0.05	0.5	0.05	0.1	3.9		
28	6	0.05	0.5	0.05	0.3	17.5	0.2	13.6
29	1	-0-	0.5	-0-	0.0	2.7		
30	6	-0-	0.5	-0-	0.0	9.4	0.0	6.7
31	1	-0-	0.5	0.05	0.0	3.5		
32	6	-0-	0.5	0.05	0.0	17.0	0.0	13.5
33	1	-0-	-0-	0.05	0.0	-0.3		
34	6	-0-	-0-	0.05	0.0	-1.3	0.0	-1.0

Appendix Table 24. Conditions, Treatments and Results of Experiment 5-319. The pH was 5.0 ± 0.1 and the temperature was 24 - 25°C. Initial Mn, Ca, Mg and Fe content of the root material was < 0.1, 2.5, 10.5 and 0.2 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Fe+++	Mn	Ca	Mg	Fe	Mn	Ca	Mg	Fe
	hour		meq/liter				meq/kg				meq/kg/5hr		
1	1	0.05	-0-	-0-	-0-	1.7			0.0				
2	6	0.05	-0-	-0-	-0-	4.5			0.0	2.8			0.0
3	1	0.05	-0-	-0-	0.001	1.7			0.0				
4	6	0.05	-0-	-0-	0.001	4.9			0.0	3.2			0.0
5	1	0.05	-0-	-0-	0.005	1.8			0.5				
6	6	0.05	-0-	-0-	0.005	4.8			1.1	3.0			0.6
7	1	0.05	-0-	-0-	0.01	1.8			1.0				
8	6	0.05	-0-	-0-	0.01	4.9			3.6	3.1			2.6
13	1	0.05	0.05	-0-	-0-	1.1	0.0		0.1				
14	6	0.05	0.05	-0-	-0-	4.1	0.0		0.0	3.0	0.0		-0.1
15	1	0.05	0.05	-0-	0.001	1.1	0.0		0.0				
16	6	0.05	0.05	-0-	0.001	4.3	0.0		0.0	3.2	0.0		0.0
17	1	0.05	0.05	-0-	0.005	1.1	0.0		0.5				
18	6	0.05	0.05	-0-	0.005	4.2	0.0		1.0	3.1	0.0		0.5
19	1	0.05	0.05	-0-	0.01	1.1	0.0		1.1				
20	6	0.05	0.05	-0-	0.01	4.3	0.0		3.4	3.2	0.0		2.3
25	1	0.05	-0-	0.05	-0-	1.0		-0.7	-0.1				
26	6	0.05	-0-	0.05	-0-	2.7		-0.9	-0.1	1.7		-0.2	0.0
27	1	0.05	-0-	0.05	0.001	1.1		-0.6	-0.1				
28	6	0.05	-0-	0.05	0.001	2.7		-0.7	-0.1	1.6		-0.1	0.0
29	1	0.05	-0-	0.05	0.005	1.1		-0.9	0.4				
30	6	0.05	-0-	0.05	0.005	2.8		-0.9	1.0	1.7		0.0	0.6
31	1	0.05	-0-	0.05	0.01	1.1		-0.4	1.2				
32	6	0.05	-0-	0.05	0.01	2.7		-0.9	3.7	1.6		-0.5	2.5
37	1	-0-	-0-	-0-	0.01	0.0			1.1				
39	6	-0-	-0-	-0-	0.01	0.0			3.7				2.6

Appendix Table 25. Conditions, Treatments and Results of Experiment 5-23. The pH was 5.0 - 5.3 and the temperature was 24.5 - 25°C. Initial Mn and K content of the root material was < 0.1 and 19.7 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition		Uptake		Absorption Rate	
		Mn	K	Mn	K	Mn	K
	hour	meq/liter		meq/kg		meq/kg/5hr	
1	1	0.05	-0-	1.9	-0.9		
2	6	0.05	-0-	5.0	-0.7	3.1	0.2
3	1	0.05	0.001	1.8	-0.5		
4	6	0.05	0.001	4.9	0.2	3.1	0.7
5	1	0.05	0.01	1.5	1.9		
6	6	0.05	0.01	4.0	7.0	2.5	5.1
7	1	0.05	0.1	1.5	2.0		
8	6	0.05	0.1	2.8	9.7	1.3	7.7
9	1	0.05	1.0	1.0	5.3		
10	6	0.05	1.0	1.9	27.1	0.9	21.8

Appendix Table 26. Conditions, Treatments and Results of Experiment 5-36. The pH was 5.0 - 5.6 and the temperature was 24.5 - 25°C. Initial Mn, Ca and K content of the root material was < 0.1, 2.6 and 20.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	K	Mn	Ca	K	Mn	Ca	K
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	2.0		-0.7			
2	6	0.05	-0-	-0-	3.4		0.7	1.4		1.4
3	1	0.05	-0-	0.01	1.6		1.8			
4	6	0.05	-0-	0.01	2.7		6.9	1.1		5.1
5	1	0.05	-0-	0.05	1.5		2.2			
6	6	0.05	-0-	0.05	2.1		9.9	0.6		7.7
7	1	0.05	-0-	0.1	1.5		2.2			
8	6	0.05	-0-	0.1	2.2		7.3	0.7		5.1
9	1	0.05	-0-	0.5	1.4		5.2			
10	6	0.05	-0-	0.5	1.9		17.5	0.5		12.3
11	1	0.05	-0-	1.0	1.1		5.8			
12	6	0.05	-0-	1.0	1.5		22.7	0.4		16.9
13	1	0.05	-0-	5.0	0.5		10.6			
14	6	0.05	-0-	5.0	1.1		33.2	0.6		22.6
15	1	0.05	0.5	-0-	0.4	1.0	-0.7			
16	6	0.05	0.5	-0-	2.3	0.6	-1.1	1.9	-0.4	0.4
17	1	0.05	0.5	0.01	0.3	0.9	1.8			
18	6	0.05	0.5	0.01	1.8	0.6	7.3	1.5	-0.3	5.5
19	1	0.05	0.5	0.05	0.2	0.7	3.7			
20	6	0.05	0.5	0.05	0.6	0.2	19.7	0.4	-0.5	16.0
21	1	0.05	0.5	0.1	0.2	0.7	3.7			
22	6	0.05	0.5	0.1	0.6	0.2	22.7	0.4	-0.5	19.0
23	1	0.05	0.5	0.5	0.2	0.7	4.0			
24	6	0.05	0.5	0.5	0.7	0.2	19.7	0.5	-0.5	15.7
25	1	0.05	0.5	1.0	0.2	0.6	5.2			
26	6	0.05	0.5	1.0	0.6	0.1	27.0	0.4	-0.5	21.8
27	1	0.05	0.5	5.0	0.2	0.2	9.9			
28	6	0.05	0.5	5.0	0.4	-0.3	39.8	0.2	-0.5	29.9

Appendix Table 27. Conditions, Treatments and Results of Experiment 5-39. The pH was 5.0 ± 0.1 and the temperature was 25 - 25.5°C. Initial Mn, Ca and Rb content of the root material was < 0.1, 2.4 and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	Rb	Mn	Ca	Rb	Mn	Ca	Rb
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	1.9		0.0			
2	6	0.05	-0-	-0-	4.8		0.0	2.7		0.0
3	1	0.05	-0-	0.005	1.7		1.9			
4	6	0.05	-0-	0.005	5.1		4.6	3.4		2.7
5	1	0.05	-0-	0.01	1.7		2.9			
6	6	0.05	-0-	0.01	4.3		8.6	2.6		5.7
7	1	0.05	-0-	0.05	1.6		4.4			
8	6	0.05	-0-	0.05	3.5		12.7	1.9		8.3
9	1	0.05	-0-	0.1	1.6		4.7			
10	6	0.05	-0-	0.1	3.7		13.3	2.1		8.6
11	1	0.05	-0-	0.5	1.5		5.1			
12	6	0.05	-0-	0.5	3.5		14.3	2.0		9.2
13	1	0.05	-0-	1.0	1.2		5.4			
14	6	0.05	-0-	1.0	3.1		15.9	1.9		10.5
15	1	0.05	0.5	-0-	0.4	1.1	0.0			
16	6	0.05	0.5	-0-	3.0	1.3	0.0	2.6	0.2	0.0
17	1	0.05	0.5	0.005	0.4	1.0	1.7			
18	6	0.05	0.5	0.005	3.5	1.4	4.4	3.1	0.4	2.7
19	1	0.05	0.5	0.01	0.4	1.0	2.7			
20	6	0.05	0.5	0.01	3.0	1.1	7.7	2.6	0.1	5.0
21	1	0.05	0.5	0.05	0.2	0.9	4.6			
22	6	0.05	0.5	0.05	1.1	1.0	15.0	0.9	0.1	10.4
23	1	0.05	0.5	0.1	0.3	0.9	5.0			
24	6	0.05	0.5	0.1	1.1	1.0	16.0	0.8	0.1	11.0
25	1	0.05	0.5	0.5	0.3	0.9	6.0			
26	6	0.05	0.5	0.5	1.1	1.0	17.6	0.8	0.1	11.6
27	1	0.05	0.5	1.0	0.2	0.9	6.7			
28	6	0.05	0.5	1.0	1.2	0.9	18.4	1.0	0.0	11.7

Appendix Table 28. Conditions, Treatments and Results of Experiment 6-107. The pH was 4.9 - 5.2 and the temperature was 24.5 - 25°C. Initial Mn, Ca, Mg and Rb content of the root material was < 0.1, 2.4, 9.1 and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Rb	Mn	Ca	Mg	Rb	Mn	Ca	Mg	Rb
	hour	meq/liter				meq/kg				meq/kg/5hr			
1	1	0.05	-0-	-0-	-0-	1.8			0.0				
2	6	0.05	-0-	-0-	-0-	4.4			0.0	2.6			0.0
3	1	0.05	-0-	-0-	0.001	1.7			0.6				
4	6	0.05	-0-	-0-	0.001	4.6			1.1	2.9			0.5
5	1	0.05	-0-	-0-	0.005	1.7			1.7				
6	6	0.05	-0-	-0-	0.005	4.5			4.6	2.8			2.9
7	1	0.05	-0-	-0-	0.01	1.7			2.8				
8	6	0.05	-0-	-0-	0.01	4.0			8.1	2.3			5.3
9	1	0.05	-0-	-0-	0.05	1.7			4.2				
10	6	0.05	-0-	-0-	0.05	3.4			12.2	1.7			8.0
11	1	0.05	-0-	-0-	0.1	1.6			4.6				
12	6	0.05	-0-	-0-	0.1	3.7			12.7	2.1			8.1
13	1	0.05	0.05	-0-	-0-	1.1	-0.1		0.0				
14	6	0.05	0.05	-0-	-0-	3.3	0.0		0.0	2.2	0.1		0.0
15	1	0.05	0.05	-0-	0.001	1.1	-0.1		0.4				
16	6	0.05	0.05	-0-	0.001	3.6	0.0		1.0	2.5	0.1		0.6
17	1	0.05	0.05	-0-	0.005	0.9	-0.2		2.8				
18	6	0.05	0.05	-0-	0.005	3.5	-0.1		4.9	2.6	0.1		2.1

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Appendix Table 28. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Rb	Mn	Ca	Mg	Rb	Mn	Ca	Mg	Rb
	hour	meq/liter				meq/kg				meq/kg/5hr			
19	1	0.05	0.05	-0-	0.01	1.0	-0.2		1.9				
20	6	0.05	0.05	-0-	0.01	2.9	-0.2		8.6	1.9	0.0		6.7
21	1	0.05	0.05	-0-	0.05	0.9	-0.3		4.6				
22	6	0.05	0.05	-0-	0.05	1.9	-0.3		13.5	1.0	0.0		8.9
23	1	0.05	0.05	-0-	0.1	0.9	-0.3		4.8				
24	6	0.05	0.05	-0-	0.1	2.2	-0.3		14.2	1.3	0.0		9.4
25	1	0.05	-0-	0.05	-0-	1.2		-0.6	0.0				
26	6	0.05	-0-	0.05	-0-	3.1		-0.6	0.0	1.9		0.0	0.0
27	1	0.05	-0-	0.05	0.001	1.2		-0.8	0.5				
28	6	0.05	-0-	0.05	0.001	3.0		-0.8	1.1	1.8		0.0	0.6
29	1	0.05	-0-	0.05	0.005	1.1		-0.9	1.9				
30	6	0.05	-0-	0.05	0.005	2.8		-0.9	4.8	1.7		0.0	2.9
31	1	0.05	-0-	0.05	0.01	1.1		-1.0	3.0				
32	6	0.05	-0-	0.05	0.01	2.5		-0.8	8.7	1.4		0.2	5.7
33	1	0.05	-0-	0.05	0.05	1.1		-0.6	4.8				
34	6	0.05	-0-	0.05	0.05	2.1		-1.1	13.0	1.0		-0.5	8.2
35	1	0.05	-0-	0.05	0.1	1.0		-0.6	5.0				
36	6	0.05	-0-	0.05	0.1	2.2		-0.8	13.5	1.2		-0.2	8.5
37	1	-0-	-0-	-0-	0.05	0.0		-1.1	3.6				
38	6	-0-	-0-	-0-	0.05	0.0		-2.1	8.5			-1.0	4.9

Appendix Table 29. Conditions, Treatments and Results of Experiment 5-37. The pH was 4.9 - 5.3 and the temperature was 24.5 - 25°C. Initial Mn, Ca and Na content of the root material was < 0.1, 2.4 and 1.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	Na	Mn	Ca	Na	Mn	Ca	Na
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	2.2		-0.1			
2	6	0.05	-0-	-0-	5.1		-0.1	2.9		0.0
3	1	0.05	-0-	0.01	1.9		0.2			
4	6	0.05	-0-	0.01	5.1		1.3	3.2		1.1
5	1	0.05	-0-	0.05	2.0		1.5			
6	6	0.05	-0-	0.05	4.2		5.8	2.2		4.3
7	1	0.05	-0-	0.10	1.9		2.2			
8	6	0.05	-0-	0.10	4.0		9.3	2.1		7.1
9	1	0.05	-0-	0.50	1.4		4.3			
10	6	0.05	-0-	0.50	3.2		18.3	1.8		14.0
11	1	0.05	-0-	1.0	1.3		5.5			
12	6	0.05	-0-	1.0	3.0		22.0	1.7		16.5
13	1	0.05	-0-	5.0	0.7		9.2			
14	6	0.05	-0-	5.0	1.8		39.0	1.1		29.8
15	1	0.05	0.5	-0-	0.5	1.0	-0.1			
16	6	0.05	0.5	-0-	3.5	0.9	-0.1	3.0	-0.1	0.0
17	1	0.05	0.5	0.01	0.5	0.9	0.0			
18	6	0.05	0.5	0.01	3.2	1.0	0.9	2.7	0.1	0.9
19	1	0.05	0.5	0.05	0.4	0.5	0.6			
20	6	0.05	0.5	0.05	2.9	0.8	5.0	2.5	0.3	4.6
21	1	0.05	0.5	0.10	0.4	0.5	1.6			
22	6	0.05	0.5	0.10	2.4	0.7	8.0	2.0	0.2	6.4
23	1	0.05	0.5	0.50	0.3	0.7	3.8			
24	6	0.05	0.5	0.50	1.8	0.8	18.9	1.5	0.1	15.1
25	1	0.05	0.5	1.0	0.4	0.6	5.0			
26	6	0.05	0.5	1.0	1.7	0.6	23.3	1.3	0.0	18.3
27	1	0.05	0.5	5.0	0.4	0.1	7.8			
28	6	0.05	0.5	5.0	1.1	0.1	37.9	0.7	0.0	30.1

Appendix Table 30. Conditions, Treatments and Results of Experiment 6-108. The pH was 4.9 - 5.2 and the temperature was 25 ± 0.5°C. Initial Mn, Ca, Mg and Na content of the root material was < 0.1, 2.9, 11.0 and 0.9 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Na	Mn	Ca	Mg	Na	Mn	Ca	Mg	Na
	hour	meq/liter				meq/kg				meq/kg/5hr			
1	1	0.05	-0-	-0-	-0-	1.7			0.0				
2	6	0.05	-0-	-0-	-0-	4.1			-0.2	2.4			-0.2
3	1	0.05	-0-	-0-	0.001	1.7			-0.2				
4	6	0.05	-0-	-0-	0.001	4.0			-0.2	2.3			0.0
5	1	0.05	-0-	-0-	0.005	1.8			0.1				
6	6	0.05	-0-	-0-	0.005	4.2			0.3	2.4			0.2
7	1	0.05	-0-	-0-	0.01	1.9			0.3				
8	6	0.05	-0-	-0-	0.01	4.1			0.8	2.2			0.5
9	1	0.05	-0-	-0-	0.05	1.7			1.3				
10	6	0.05	-0-	-0-	0.05	3.8			4.1	2.1			2.8
11	1	0.05	-0-	-0-	0.1	1.6			2.0				
12	6	0.05	-0-	-0-	0.1	3.6			6.1	2.0			4.1
13	1	0.05	0.05	-0-	-0-	1.0	-0.3		-0.2				
14	6	0.05	0.05	-0-	-0-	3.1	-0.3		-0.2	2.1	0.0		0.0
15	1	0.05	0.05	-0-	0.001	1.1	-0.3		0.0				
16	6	0.05	0.05	-0-	0.001	3.1	-0.3		-0.2	2.0	0.0		-0.2
17	1	0.05	0.05	-0-	0.005	1.1	-0.3		0.1				
18	6	0.05	0.05	-0-	0.005	3.0	-0.3		0.3	1.9	0.0		0.2

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Appendix Table 30. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Na	Mn	Ca	Mg	Na	Mn	Ca	Mg	Na
	hour	meq/liter				meq/kg				meq/kg/5hr			
19	1	0.05	0.05	-0-	0.01	1.1	-0.4		0.1				
20	6	0.05	0.05	-0-	0.01	2.9	-0.3		0.7	1.8	0.1		0.6
21	1	0.05	0.05	-0-	0.05	1.1	-0.3		1.0				
22	6	0.05	0.05	-0-	0.05	2.6	-0.3		4.0	1.5	0.0		3.0
23	1	0.05	0.05	-0-	0.1	1.0	-0.4		2.0				
24	6	0.05	0.05	-0-	0.1	2.4	-0.2		5.8	1.4	0.2		3.8
25	1	0.05	-0-	0.05	-0-	1.2		-0.7	0.0				
26	6	0.05	-0-	0.05	-0-	2.9		-1.1	-0.2	1.7		-0.4	-0.2
27	1	0.05	-0-	0.05	0.001	1.2		-0.8	-0.2				
28	6	0.05	-0-	0.05	0.001	2.8		-1.2	-0.2	1.6		-0.4	0.0
29	1	0.05	-0-	0.05	0.005	1.2		-1.1	0.1				
30	6	0.05	-0-	0.05	0.005	2.8		-1.2	0.3	1.6		-0.1	0.2
31	1	0.05	-0-	0.05	0.01	1.2		-0.7	0.3				
32	6	0.05	-0-	0.05	0.01	2.8		-1.6	0.8	1.6		-0.9	0.5
33	1	0.05	-0-	0.05	0.05	1.2		-0.7	1.1				
34	6	0.05	-0-	0.05	0.05	2.6		-1.2	4.0	1.4		-0.5	2.9
35	1	0.05	-0-	0.05	0.1	1.1		-0.7	2.0				
36	6	0.05	-0-	0.05	0.1	2.5		-1.6	6.4	1.4		-0.9	4.4
37	1	-0-	-0-	-0-	0.05			-1.2	0.7				
38	6	-0-	-0-	-0-	0.05			-3.2	0.8			-2.0	0.1

Appendix Table 31. Conditions, Treatments and Results of Experiment 5-310. The pH was 5.0 - 5.2 and the temperature was 24 - 25°C. Initial Mn, Ca and Li content of the root material was < 0.1, 2.5 and 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Mn	Ca	Li	Mn	Ca	Li	Mn	Ca	Li
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	0.05	-0-	-0-	2.2		0.0			
2	6	0.05	-0-	-0-	5.2		0.0	3.0		0.0
3	1	0.05	-0-	0.005	2.2		0.0			
4	6	0.05	-0-	0.005	5.1		0.0	2.9		0.0
5	1	0.05	-0-	0.01	2.2		0.0			
6	6	0.05	-0-	0.01	5.4		0.0	3.2		0.0
7	1	0.05	-0-	0.05	2.2		0.0			
8	6	0.05	-0-	0.05	5.4		0.1	3.2		0.1
9	1	0.05	-0-	0.1	2.2		0.2			
10	6	0.05	-0-	0.1	5.5		0.4	3.3		0.2
11	1	0.05	-0-	0.5	1.9		0.6			
12	6	0.05	-0-	0.5	6.0		1.7	4.1		1.1
13	1	0.05	-0-	1.0	1.9		1.0			
14	6	0.05	-0-	1.0	6.3		3.3	4.4		2.3
15	1	0.05	0.5	-0-	0.5	1.2	0.0			
16	6	0.05	0.5	-0-	3.4	1.3	0.0	2.9	0.1	0.0
17	1	0.05	0.5	0.005	0.4	1.1	0.0			
18	6	0.05	0.5	0.005	3.5	1.3	0.0	3.1	0.2	0.0
19	1	0.05	0.5	0.01	0.4	1.2	0.0			
20	6	0.05	0.5	0.01	3.5	1.4	0.0	3.1	0.2	0.0
21	1	0.05	0.5	0.05	0.4	1.1	0.0			
22	6	0.05	0.5	0.05	3.5	1.3	0.1	3.1	0.2	0.1
23	1	0.05	0.5	0.1	0.4	1.2	0.0			
24	6	0.05	0.5	0.1	3.5	1.3	0.0	3.1	0.1	0.0
25	1	0.05	0.5	0.5	0.5	1.0	0.0			
26	6	0.05	0.5	0.5	3.5	1.2	0.3	3.0	0.2	0.3
27	1	0.05	0.5	1.0	0.5	1.1	0.2			
28	6	0.05	0.5	1.0	3.7	1.4	0.9	3.2	0.3	0.7

Appendix Table 32. Conditions, Treatments and Results of Experiment 6-109. The pH was 4.9 - 5.2 and the temperature was 25 ± 0.5°C. Initial Mn, Ca, Mg and Li content of the root material was < 0.1, 2.6, 9.8 and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Li	Mn	Ca	Mg	Li	Mn	Ca	Mg	Li
	hour	meq/liter				meq/kg				meq/kg/5hr			
1	1	0.05	-0-	-0-	-0-	1.9			0.0				
2	6	0.05	-0-	-0-	-0-	4.3			0.0	2.4			0.0
3	1	0.05	-0-	-0-	0.001	1.9			0.0				
4	6	0.05	-0-	-0-	0.001	4.5			0.0	2.6			0.0
5	1	0.05	-0-	-0-	0.01	2.0			0.0				
6	6	0.05	-0-	-0-	0.01	4.5			0.0	2.5			0.0
7	1	0.05	-0-	-0-	0.1	1.9			0.0				
8	6	0.05	-0-	-0-	0.1	4.6			0.2	2.7			0.2
9	1	0.05	-0-	-0-	1.0	1.7			0.7				
10	6	0.05	-0-	-0-	1.0	4.7			2.5	3.0			1.8
11	1	0.05	-0-	-0-	10	0.5			5.4				
12	6	0.05	-0-	-0-	10	1.8			19.6	1.3			14.2
13	1	0.05	0.05	-0-	-0-	1.1	-0.3		0.0				
14	6	0.05	0.05	-0-	-0-	3.5	-0.3		0.0	2.4	0.0		0.0
15	1	0.05	0.05	-0-	0.001	1.1	-0.3		0.0				
16	6	0.05	0.05	-0-	0.001	3.3	-0.3		0.0	2.2	0.0		0.0
17	1	0.05	0.05	-0-	0.01	1.1	-0.3		0.0				
18	6	0.05	0.05	-0-	0.01	3.6	-0.3		0.0	2.5	0.0		0.0

Continued on next page

Appendix Table 32. (continued)

Trmt. No.	Time	Trmt. Soln. Composition				Uptake				Absorption Rate			
		Mn	Ca	Mg	Li	Mn	Ca	Mg	Li	Mn	Ca	Mg	Li
	hour	meq/liter				meq/kg				meq/kg/5hr			
19	1	0.05	0.05	-0-	0.1	1.1	-0.3		0.0				
20	6	0.05	0.05	-0-	0.1	3.4	-0.3		0.1	2.3	0.0		0.1
21	1	0.05	0.05	-0-	1.0	1.0	-0.4		0.5				
22	6	0.05	0.05	-0-	1.0	3.9	-0.3		1.1	2.9	0.1		0.6
23	1	0.05	0.05	-0-	10	0.5	-0.8		4.2				
24	6	0.05	0.05	-0-	10	2.9	-0.7		11.4	2.4	0.1		7.2
25	1	0.05	-0-	0.05	-0-	1.1		-0.9	0.0				
26	6	0.05	-0-	0.05	-0-	2.7		-0.9	0.0	1.6		0.0	0.0
27	1	0.05	-0-	0.05	0.001	1.1		-0.9	0.0				
28	6	0.05	-0-	0.05	0.001	2.7		-1.0	0.0	1.6		-0.1	0.0
29	1	0.05	-0-	0.05	0.01	1.3		-0.8	0.0				
30	6	0.05	-0-	0.05	0.01	2.9		-0.8	0.0	1.6		0.0	0.0
31	1	0.05	-0-	0.05	0.1	1.2		-1.0	0.1				
32	6	0.05	-0-	0.05	0.1	2.8		-0.8	0.3	1.6		0.2	0.2
33	1	0.05	-0-	0.05	1.0	1.0		-1.0	0.7				
34	6	0.05	-0-	0.05	1.0	2.6		-0.6	2.6	1.6		0.4	1.9
35	1	0.05	-0-	0.05	10	0.5		-1.0	5.3				
36	6	0.05	-0-	0.05	10	1.5		-0.9	19.2	1.0		0.1	13.9
37	1	-0-	-0-	-0-	1.0			-1.7	2.1				
38	6	-0-	-0-	-0-	1.0			-2.0	6.7			-0.3	4.6

Appendix Table 33. Conditons, Treatments and Results of Experiment 4-211. The pH was 4.9 - 5.2 and the temperature was 25 - 25.5°C. Initial Li, Mg and Mn content of the root material was < 0.1, 10.2 and < 0.1 meq/kg respectively. All ions were provided in the treatment solution as chloride salts.

Trmt. No.	Time	Trmt. Soln. Composition			Uptake			Absorption Rate		
		Li	Mg	Mn	Li	Mg	Mn	Li	Mg	Mn
	hour	meq/liter			meq/kg			meq/kg/5hr		
1	1	5	-0-	-0-	4.6		0.0			
2	6	5	-0-	-0-	16.4		0.0	11.8		0.0
3	1	5	-0-	0.1	2.9		1.2			
4	6	5	-0-	0.1	9.7		6.8	6.8		5.6
5	1	5	-0-	0.5	1.9		2.4			
6	6	5	-0-	0.5	6.5		12.2	4.6		9.8
7	1	5	-0-	1.0	1.3		2.8			
8	6	5	-0-	1.0	5.2		14.7	3.9		11.9
9	1	5	-0-	5	1.0		4.1			
10	6	5	-0-	5	3.2		17.7	2.2		13.6
11	1	5	-0-	10	0.7		4.4			
12	6	5	-0-	10	2.6		18.4	1.9		14.0
13	1	5	-0-	25	0.8		5.9			
14	6	5	-0-	25	1.9		21.0	1.1		15.1
15	1	5	5	0	1.3	2.7	0.0			
16	6	5	5	0	8.8	16.0	0.0	7.5	13.3	0.0
17	1	5	5	0.1	1.3	2.1	0.2			
18	6	5	5	0.1	8.6	10.4	0.8	7.3	8.3	0.6
19	1	5	5	0.5	1.2	1.7	0.6			
20	6	5	5	0.5	7.5	6.1	2.2	6.3	4.4	1.6
21	1	5	5	1.0	1.2	1.3	0.9			
22	6	5	5	1.0	5.5	4.0	2.9	4.3	2.7	2.0
23	1	5	5	5	0.9	0.4	2.5			
24	6	5	5	5	4.2	2.5	7.5	3.3	2.1	5.0
25	1	5	5	10	0.9	0.3	3.4			
26	6	5	5	10	3.4	1.7	9.5	2.5	1.4	6.1
27	1	5	5	25	0.8	-0.1	5.0			
28	6	5	5	25	2.4	0.7	12.8	1.6	0.8	7.8