STUDIES OF CATION ABSORPTION BY SOME FLORICULTURE CROPS

BY

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

An understanding of the selective absorption of mineral nutrients by plants is one of the challenging problems of plant nutrition. Investigators have employed many approaches in an attempt to solve this problem.

It was inevitable with increasing knowledge of ionic exchange, and with the prominence of exchange phenomena in soil studies, that attempts be made to relate the exchange reaction of plant roots to selective absorption. Many investigators have been aware of the fact that exchange reactions might be important in nutrient absorption by plant roots. However, there was no way to test the hypothesis until some means of evaluating the exchange capacity of plant roots was developed. Mattson et al (29) were the first to develop a method for quantitatively evaluating the relative exchange capacities of plant roots. Drake (10) and Graham (16) both have developed modified methods for use with fresh tissue.

The purpose of this investigation was to determine the relative exchange capacity of the roots of some floriculture crops and try to relate this information to their selective cation absorption. A relationship between the relative exchange capacity and selective cation absorption could aid in predicting the fertilizer needs of floriculture crops under varying soil conditions. Information about the actual nutrient requirements of floriculture crops together with information about the feeding power of roots of these crops for different nutrient elements could aid in a better understanding of the nutritional problems of commercial growers.

REVIEW OF LITERATURE

Theories of Ion Absorption

One of the most widely studied theories of ion absorption in plants is the anion respiration or salt respiration theory of Lundegardh (7, 27). Lundegardh found in wheat that anion intake was related to aerobic respiration. A neutral salt such as potassium chloride, increased the respiration rate in the cells of plant roots with an accompanying increase in salt absorption. The fraction of the respiration of root cells which was stimulated by the added salt, was very sensitive to cyanide. Cyanide inhibited both this fraction of the cell respiration and salt accumulation in the root cells. Lundegardh concluded this was probably the cytochrome-cytochrome oxidase system which was involved. He postulated that at the cytochrome stage, hydrogen ions, and electrons derived from hydrogen atoms of respiratory substrates, were separated. The cytochrome could pass electrons in one direction and anions in the opposite direction thru the cytoplasm of the cell due to the valence change of the iron atom in the cytochrome. The liberated hydrogen ions could pass out of the cell in exchange for cations.

If this hypothesis is valid, the quotient (equivalent absorbed anions/ molecules of oxygen consumed) should have a constant value. Since twenty-four steps of electron transfer are concerned in the complete oxidation of glucose, $q(an/O_2)$ should have a value of 4. This theoretical value was approached in experiments with storage tissue of carrot roots by Robertson and Wilkens (41). Lundegardh found much lower values for the $q(an/O_2)$ with wheat roots. He attributed possible sources of error to loss of anions by bleeding of the excised roots, possible internal transport of mineral and organic anions, and different types of anion respiration in different zones of the root system.

Overstreet and Jacobson (34) have reviewed different theories of ion absorption by plant roots and have proposed a theory which they feel best explains known observations. According to Overstreet and Jacobson, the first step in ion absorption by roots is an ionic exchange reaction between plant tissues and the substrate. Cation and anion exchange are somewhat independent of each other, but of a similar mechanism. Hydrogen ions of the plant roots are exchanged for cations of the substrate. The exchange reaction involved in anion exchange is not understood. The cell vacuole is connected to the culture medium by a system which fails to allow the passage of mineral ions except in connection with an organic carrier. Mineral cations and anions are bound to organic carriers and pass thru the connecting link into the cell vacuole where they are again released. The ion transport across the connecting link and release on the innerside into the cell vacuole is accomplished by certain respiratory reactions. Ions which are transported by the same organic compounds interfere with the absorption of each other.

Schuffelen (43) also proposed ion exchange between the plant roots and the substrate as the first step in ion absorption. Ion absorption is the result of the physical-chemical activity of the ions on the periphery of the root and the ions of the substrate. A difference in ion activity causes a flow of ions to move in the direction of the root and the flow is maintained by transport and inactivation of ions taken into the plant. A complication of the process in question arises from exchange reactions between the cell wall of the root and the substrate which Schuffelen refers to as the surface function. The surface function or surface reaction is of a non-living nature and is regulated by the composition of the plasma of the root wall. The composition of the plasma of the root cell walls is highly important in connection with a study of the significance of the ion ratio of the substrate in relation to plant growth.

The transport of ions into the plant is related to the metabolism of the plant and affects the overall ion intake by the plant.

Epstein and Hagen (13) have derived a theory, similar in many respects to that of Jacobson and Overstreet (34), from observations of the velocity of the absorption reaction of excised barley roots for alkali cations. They visualize fixed sites on the root cell which bind specific cations. Cations which compete for the same sites interfere with the absorption of each other.

Cooper (8) arranged the soil elements in the order of decreasing standard electrode potentials. He observed that the intensity of removal of ions from soil colloids and plant tissue by electrodialysis was in the same order as their standard electrode potentials. He observed that the average percent composition of a great many species of plants also tends to follow the same general order of decreasing standard electrode potentials.

He attempted to relate nutrient absorption to what he terms capacity and intensity of the ions in the soil. Capacity would be the amount available in the soil related to the solubility of soil minerals. Intensity would be the activity of the specific ions related to the standard electrode potentials.

Breazeale et al (6) have proposed that ion absorption in plants is an electrical phenomena. Ions migrate toward plant roots in response to an electrical impulse generated by the plant. Using the plant as one electrode, they were able to show that all ions possess a half wave potential, which is about half their standard electrode potential, and at which electromotive force their conductance and migration velocity reach a maximum.

Theories of Ion Exchange

Kunin and Meyers (25) describe several theories of ion exchange in regard to exchange resins. The crystal lattice theory applies to ion exchange between ionic solids and the surrounding solution. The ion at the surface of the crystal has less internal attractive forces holding it in the lattice than internal ions. Polar molecules, such as water, exert an attractive force on these surface ions which may be sufficient to dislodge them from the crystal structure so that another ion from the solution can enter the crystal lattice.

The double layer theory of ion exchange, originally proposed by Helmholtz and modified by Gouy (30), visualizes a colloidal particle as surrounded by an ionic atmosphere of electrostatically attracted ions. This ionic atmosphere along with the attracted waters of hydration moves with the particle thru the solution. Ions from the free solution are continually exchanging with ions of the ionic atmosphere. While the crystal lattice theory assumes a fixed number of exchange sites on the colloidal particle which must be satisfied, the extent of the ionic atmosphere of the double layer is dependent both upon the concentration and pH of the surrounding solution.

A third theory of ion exchange applies the Theory of Donnan distribution to colloidal systems (30). The colloidal particle is considered the non-diffusible ion. Transfer of ions must occur between the colloidal micelle and the solution until the concentrations of all diffusible ions, expressed as activities, are the same in both phases. The ratio of different ions within the colloidal micelle is then governed by the attraction of the colloidal particle for the specific ion and the laws of Donnan distribution.

Plant Roots and Ionic Exchange

Devaux (9), a French chemist, was able to show in 1916 that plant roots exhibit cation exchange properties. Pectins in the roots were thought to be the seat of the exchange sites.

Mattson et al (28) were the first to develop a method for determining the exchange capacity of plant roots. The roots were electrodialized, dried and ground. A weighed amount of dried roots was then placed in normal potassium chloride solution and titrated with potassium hydroxide. Pea, rye, and barley roots were found to have exchange capacities in the order of 71, 29.5, and 25.3 milliequivalents per 100 grams of dry weight. It was suggested that the acidoid content of the plant roots was due to the occurence of pectin in the surface layers of the roots.

Mattson (28, 29), and Elgabaly and Wiklander (12) have shown that absorption of cations in low concentration is a function of the cation-exchange capacity of the colloid and the valence of the cation. High exchange colloids show a greater attraction for divalent than monovalent ions.

Mattson et al (28) observed that in dilute solutions, the addition of calcium chloride increased the absorption of phosphorous more with pea and barley roots than did the addition of potassium chloride. They attributed this to Donnan distribution of cations in the micelles of the root colloids. The presence of the cations allows a greater concentration of the anions from the external solution in the region of the acidoid of the root surface. While these considerations would apply to the cytoplasm of the cell, Mattson suggests it would be more important in regard to the pectins in the cell walls.

Jenny and Overstreet (23) have pointed out that laws governing the interactions between colloids must be applicable to soil plant systems. Jenny (24) has visualized each adsorbed ion on a colloid as oscillating about its attraction point within a space called the oscillation cell. The volume of the oscillation cell is a constant for a particular ion adsorbed on a specific colloid. Ions from the external solution with the smaller oscillation volumes tend to displace ions adsorbed on the colloid with larger oscillation volumes by slipping between the latter and the colloid during oscillations. When two colloidal systems as soil and plant are in close contact so that the oscillation volumes of the two systems overlap, ion exchange will occur so that the oscillation volumes of the individual ions tend to become a minimum.

Direct contact exchange may occur between the ions adsorbed on soil colloids and those adsorbed on plant roots by this process without the exchanged ions passing thru the soil solution.

Williams and Coleman (51) were able to show that plant root surfaces possess exchangeable hydrogen. They interpreted the lower pH of the plant roots in comparison with the supernatent liquid to be evidence of an ionic double layer surrounding the root surface. By replacement of the hydrogen on the plant root surfaces with different cations, they were able to show that entry of cations into the root double layer follows the same type of lyotropic series as many exchange materials. Employing radioactive cesium and using corn and bean roots, they showed the first two millimeter segment including the root tip had a higher cation exchange capacity than more mature regions of the root. They stated that the nature of the cell walls in regions of cell division and enlargement were in all probability not the same as in mature cells, and that differences in the root epidermis probably accounted for differences in surface exchange properties.

Drake et al (10) determined the exchange capacity of a number of economic and weed crops by electrodializing the plant roots and titrating the exchangeable hydrogen when the dialized roots were placed in normal potassium chloride solution. Drake found that monocotyledonous plants had considerably lower cation exchange capacities than dicotyledonous plants, and that legumes, as a group, possessed high exchange capacities among the dicotyledonous plants. Drake has postulated, after the ideas of Mattson (29) and Elgabaly (12), that the exchange capacity of the root colloids determines the ratio of absorption of mono- and divalent cations at low levels of soil fertility. Plants with low root exchange capacities such as the grasses are favored in absorption of potassium over plants with high root exchange capacities such as the legumes which are characterized by a high content of calcium.

Graham and Baker (16) electrodialized plant roots for three hours at 100 volts and 0.3 amperes with the roots attached to the plant tops. They found little difference in the exchange capacity of oats, barley, rye, and wheat. The exchange capacity of soybean increased with age of plants (between four and twelve days), an increase in growing temperature and an increase in concentration of nutrient solution. They also measured the percent hydrogen saturation of the root surfaces and found it varied with nutrient treatments, age of plants, plant species, and growing temperature.

EXPERIMENTAL METHODS

Plant Material

The relative cation exchange capacities of roots of a number of floriculture plants were determined by the method outlined by Drake (10). Plants were selected for a cation absorption study whose roots had a range of cation exchange capacities and which as far as possible were of economic importance to the floriculture industry. The following plants were used: snapdragon variety Spartan Rose, chrysanthemum variety White Mefo, stock variety Shasta, (a branching type), variety H. Lavender, (a column type), and larkspur variety Light Blue. To include a monocotyledonous plant, sweet corn variety Golden Cross Bantam was used.

Ordinary cultural practices were followed in propagation and handling of the seed propagated species before they were placed in the nutrient solutions. The seeds were sown in a mixture of screened sand and soil. When seedlings were one to two inches tall, uniform plants were selected, thoroughly washed under tap water to remove soil from the roots, and placed in the different nutrient solutions of the experiment. An extra plant was placed in each jar and removed as soon as the plants became established, leaving the three most uniform plants. Corn and sweet peas were germinated in sand and seedlings transferred directly to the nutrient solution cultures. Chrysanthemum was propagated by terminal softwood cuttings from stock plants grown under continuous light. The cuttings were rooted in sand and selected plants transferred directly from the cutting bench to the nutrient solutions of the experiment.

Solution Culture

Because the determination of root exchange capacity required plant root systems free from all soil material, nutrient solution culture was employed. A table was constructed to hold thirty-four wide-mouth gallon jars. (Figure I.). The jars were fitted into a cover over the table so that the nutrient solutions were in a light-tight compartment to prevent the growth of algae. Each jar was calibrated to hold 3.6 liters of nutrient solution. Plants were supported by non-absorbent cotton packed around the stems inside of one inch diameter rubber tubing which was fitted into holes drilled into the jar lids. Aeration of the solutions was accomplished by aquarium aerating stones[1] and by sections of plastic tubing perforated on the end with a dissecting needle. The air line into each jar was regulated by a screw clamp and a continuous flow of air was bubbled thru all solutions at all times. Solutions were maintained at constant volume by frequent additions of distilled water.

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[1] Purchased from Wards Biological Establishment of Rochester, New York.

Figure I

The nutrient solution culture equipment showing the table with the gallon jars containing the nutrient solutions enclosed in a light-tight compartment.

Solution Composition

The nutrient solution developed for tomatoes by Hoagland (21) was used as a standard solution and ratios of calcium and potassium varied from this with all other ions as near constant as possible. Wide variations in the calcium-potassium ratios were used in the different treatments.

Once plants were placed in the different treatments, solutions were neither renewed nor additional nutrient added. It was realized that composition and pH of the solutions would change as the plants grew, however, it was desireable to have limited amounts of calcium and potassium available to the plants which would not have been possible if the solutions were renewed. In this manner, both the ratio of absorption and the ratio within the plant at which growth was reduced could be ascertained.

In order to maintain the same concentration of nitrogen as was present in the standard solution, ammonium nitrate was added to the solution containing the lowest concentration of calcium and potassium. With the first series of plants grown, it was observed that the low calcium and low potassium solution with the added ammonium nitrate developed a pH between 3 and 4 which was very detrimental to some species.

In order to distinguish between the effects of low calcium and low potassium, and low pH, a seventh solution was then added to the series of treatments which had calcium and potassium at the same concentration as the standard

Hoagland solution, but one-fourth of the nitrogen supplied by ammonium ions.

All of the nutrient solutions used in the experiment had the same micronutrient composition as recommended by Hoagland (21) except for iron. Iron was supplied by ferric potassium ethylene diamine tetra-acetate according to the recommendations of Jacobson (22). Each liter of nutrient solution contained approximately 5 parts per million of metallic iron. The composition of solutions employed in the experiment is given in Table 1.

Experimental Design

The design of the experiment was a random block. Each block consisted of one jar of three plants for each treatment, and blocks were replicated three times.

The dry weight and chemical analyses of the plants were determined for each replicate of each treatment. Analysis of variance was used to determine significant differences between treatment means at the 1 per cent and 5 per cent levels.

TABLE 1

THE MOLAR COMPOSITION OF THE DIFFERENT NUTRIENT SOLUTIONS EMPLOYED IN THE EXPERIMENT

Treatment[1,2]	Salts Expressed as Moles/Liter x 10^{-3}					
	KNO_3	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4$	K_2SO_4	NH_4NO_3
Low Ca:Low K		4	4	8		26
Low Ca:High K	49	4	4	8		
1 Hoagland	20	20	4	8		
High Ca:Low K		30	4	8		
High Ca:High K		30	4	8	12	
3 Hoagland	60	60	12	24		
1 Hoagland NH_4		20	4	8	10	10

[1] Micronutrients supplied by Hoagland microsolution A (21).

[2] Iron supplied by ferric potassium ethylene diamine tetra-acetate .04 grams/liter.

Growth Measurements and Harvesting Methods

Dry weight of plant tops was used to evaluate growth. Plants were harvested and tops separated from roots. Plants were harvested when root growth was sufficient to furnish 75-100 grams of roots for the determination of the root exchange capacity. Tops were placed in perforated paper bags and immediately put into a drying oven at 70° C. for forty-eight hours. Dry weights were determined on a Torsion balance to the nearest hundredth of a gram.

It was realized that the nutrient composition of plants changes with age (48), however, a comparison between different plant species was desired and it was felt that differences between different species would be of such magnitude that slight variations in physiological age at time of harvest could be neglected.

All crops were in the vegetative condition when harvested except snapdragon which had visible flower buds.

Analytical Methods

Calcium, potassium, and magnesium content of plant tissue was determined by flame spectrophotometry. Dried plant material was ground in a Wiley Mill to pass thru a 20 mesh screen. The ground tissue was placed in a drying oven at 70° C. overnight, cooled in a dissicator and one gram samples weighed in porcelain crucibles. The weighed samples were ashed in a muffle furnace at 550° C. for ten hours. The dry ash was dissolved in a slight excess of perchloric acid. Perchloric acid was used because Hinsvark et al (20) found the least amount of interference from perchlorate ions in spectrophotometric determinations. The material was then filtered thru a Whatman #2 filter paper into 100 milliliter volumetric flasks and made to volume.

Calcium and potassium were determined with a Beckman Model B spectrophotometer using acetylene as fuel. Magnesium was determined on the Beckman Model D. U. spectrophotometer using hydrogen as fuel.

Standard curves were made from known concentrations of the ion to be determined using carbonate salts neutralized with a slight excess of perchloric acid. Maximum range was selected by trial and comparison with the different plant samples to provide a standard curve which could be used to give readings within the middle two thirds for the plant samples. This portion of the curve was a straight line for calcium and magnesium and followed a smooth curve for potassium. Samples were analyzed until duplicate readings agreed within one transmission unit.

The only interference which was of sufficient magnitude to warrant correction was the increase in magnesium transmission due to potassium. A standard curve for potassium interference in the magnesium determinations was established from known amounts of potassium and magnesium and corrections made accordingly.

Determination of the Exchange Capacity of Plant Roots

The relative cation exchange capacity of the plant roots was determined by the method developed by Drake (10) with slight modifications. The determination was carried out as follows:

1. The lower two-thirds of the plant root system was washed in tap water and the coarsest roots removed. The roots were blotted dry with a paper towel and 50 grams rolled loosely in cheese cloth and secured with elastic bands at each end of the roll.
2. The roots were then placed in the center compartment of a Mattson dializing cell and the cell filled with distilled water. The Mattson cell was connected to 155 volt source of direct current. The center and cathode compartments were flushed frequently at the beginning of the dialysis so that the amperage did not exceed 2 amperes and the temperature did not exceed 40°C. The anode compartment was not flushed until near the end of the dialysis. The dialysis was continued until the amperage failed to exceed .1 ampere within a five minute period. The complete dialysis required about 50 minutes.
3. The roots were then centrifuged for five minutes at 2000 revolutions per minute to remove excess moisture and so that they would have a uniform moisture content.

4. A five gram sample (within .1 gram) was taken from the roots that were centrifuged and placed in a 400 milliliter beaker with 200 milliliters of normal potassium chloride. The roots and the potassium chloride solution was then titrated to a pH of 7 using a .02 normal sodium hydroxide. Since the end point of the titration changed with time, five minutes was used for convenience.
5. The roots were then placed in a Gooch crucible which was attached to a suction flask. A mat of larger roots was first placed in the bottom of the crucible to retain any small broken pieces. The roots were then returned to the beaker, covered with distilled water with a few drops of 1:3 hydrochloric acid and left overnight. They were then placed in a weighed Gooch crucible, washed with distilled water and oven-dried at 70°C. for twenty-four hours.
6. The dried roots were then removed from the oven and placed in a dissicator to cool. Dry weights were obtained by the use of an analytical balance.
7. The exchange capacity was calculated from the dry weight of the roots, the milliequivalents of base used in the titration and expressed as milliequivalents/100 grams of dry roots.

Modifications of Drake's procedure were largely a matter of convenience. Cheese cloth was easier to handle than the visking bags. The dialysis time was shortened by not flushing the anode compartment after each run. Employing Gooch crucibles eliminated the necessity of accurately pipetting the potassium chloride solution, evaporating the potassium chloride solution to dryness and subtracting its weight from that of the roots. It also was felt that by using small Gooch crucibles in place of the large 400 milliliter beakers, the dry roots could be weighed more accurately.

Titration curves were obtained, plotting milliliters of base versus time while keeping the pH at 7 (See Figure II). It was found that there was a large amount of initial acidity which could be titrated as fast as sodium hydroxide could be added. Further acidity seemed to be derived from equilibrium shifts from the roots and was very small in comparison with the original volume. Five minutes proved to be a convenient time in which to titrate the acidity of the supernatent liquid and the readily available acidity of the root surface.

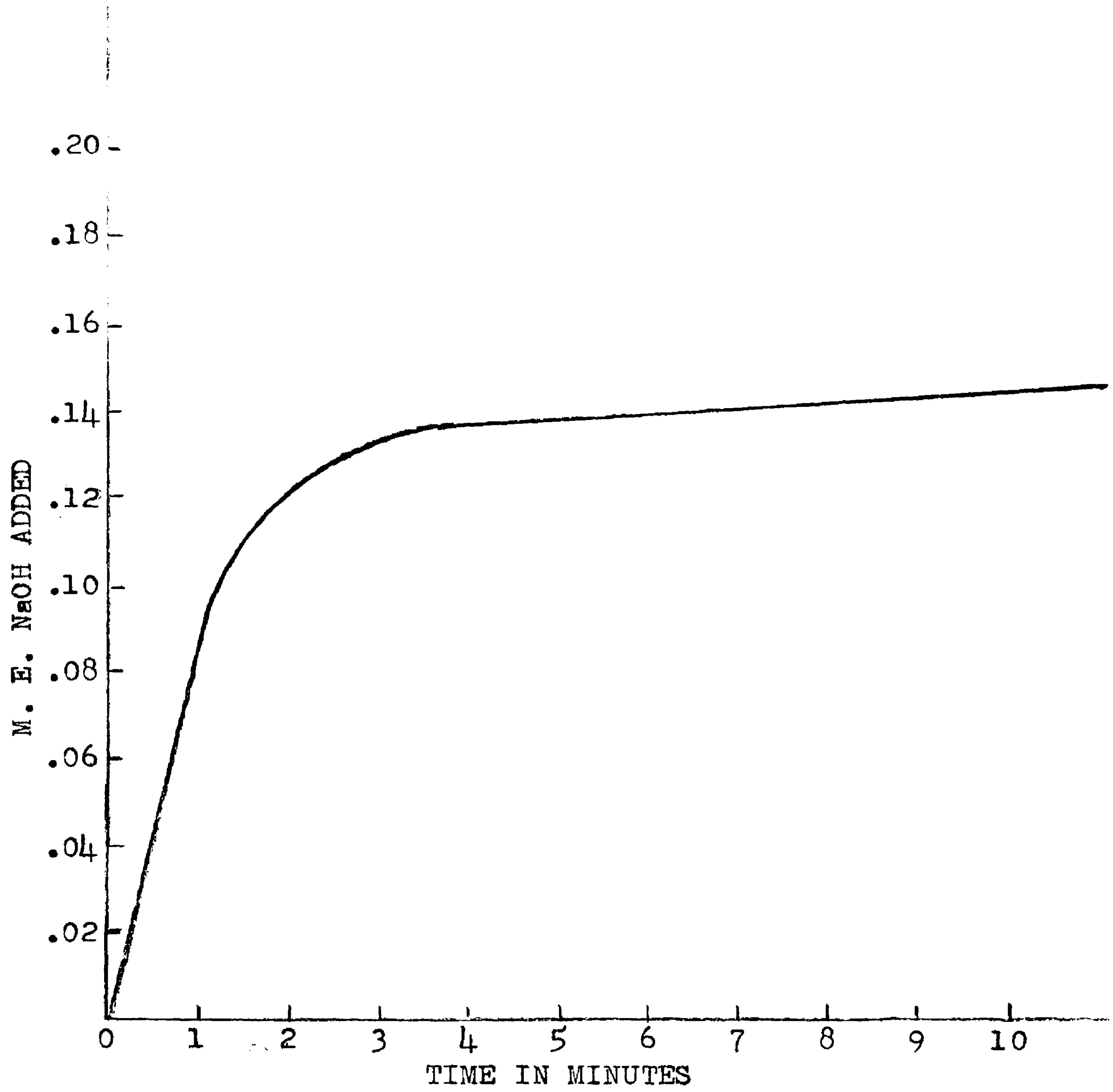

Figure II

A curve showing the amount of base necessary to maintain a pH of 7 in a solution containing 200 ml. of N KCl and 5 gms. fresh weight of dialized sweet pea roots.

Effect of Dialysis on Plant Roots

The plant roots were dialized in order to remove all exchangeable bases and leave the exchange complex saturated with hydrogen ions.

Shrinkage of the roots in the dialysis process indicated that the cell sap of the vacuole was removed along with absorbed cations. Microscopic examination of sections of dialized roots showed a disarrangement of the cells in the outer layers of the cortex.

A comparison of the titration curves of dialized and undialized sweet pea roots lends further evidence to the fact that the cell sap of the vacuole and possible other cell constiuents were removed in the dialysis (See Figure III). Five grams of both dialized and undialized sweet pea roots were immersed in 200 milliliters of normal potassium chloride solution, stirred for 30 seconds and then the supernatent liquid filtered off and titrated. The roots were then placed in a second volume of potassium chloride and left for 18 hours, again filtered and the supernatent liquid titrated.

The dialized roots show titration curves characteristic of strong acids. This would be expected in a simple exchange of potassium ions for hydrogen ions on the surface of the root colloids. The larger volume of acid displaced by the first 30 seconds immersion of the dialized roots compared to the second 18 hour immersion in the potassium chloride solutions indicated the rapidity of the exchange reaction.

This rapid exchange would be possible only if the permeability of the plant cells had been destroyed in the dialysis treatment. The fact that the pH of the potassium chloride solution failed to change with time prior to titration, indicated that the potassium and hydrogen ions were in equilibrium in the root-potassium chloride system. Neutralization of the displaced hydrogen ions caused an equilibrium shift and allowed more hydrogen to be displaced from the root colloids. As the displaced hydrogen ions were neutralized, however, the remaining hydrogen ions on the root colloid were progressively harder to displace. This assumption would account for the shape of the curve which was used to select an end point in the titration of the plant roots in the determination of the root exchange capacity (See Figure II). Milliliters of sodium hydroxide added were plotted against time. Enough base was added at one minute intervals to keep the pH of the solution at 7. The curve rises sharply at first as the easily displaced hydrogen ions are neutralized, but then levels off to a very gradual slope as the hydrogen ions become more difficult to displace from the root colloids. This makes it possible to obtain reproduceable results in measuring the relative exchange capacity of plant roots by selecting a definite time interval in which to conduct the titration.

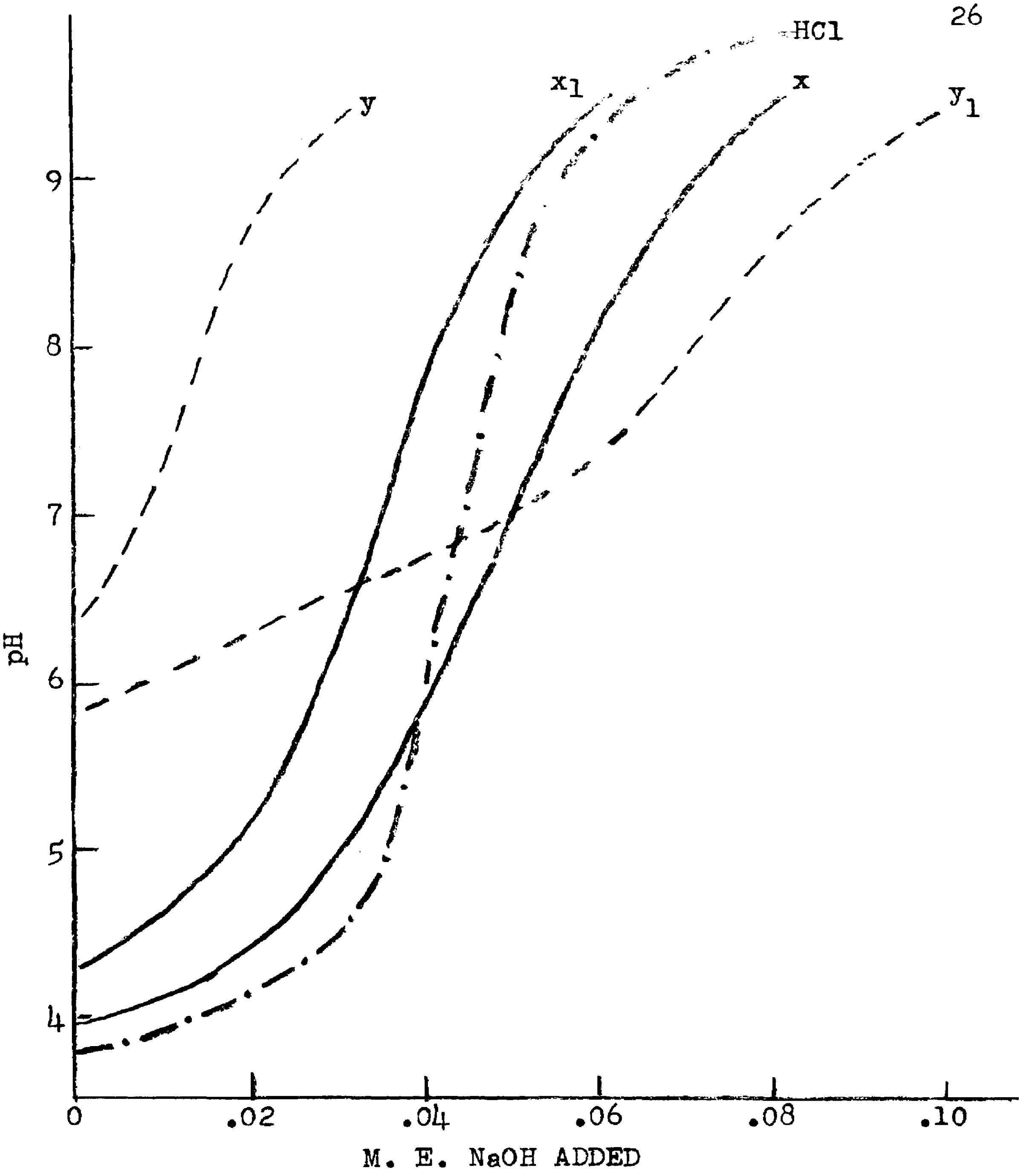

Figure III

Titration curves of the acids displaced from dialized and undialized sweet pea roots immersed for 30 second and 18 hour periods in N KCl. x - dialized roots placed in N KCl for 30 seconds. x_1 - same samples placed in N KCl for 18 hours. y - undialized roots placed in N KCl for 30 seconds. y_1 - same samples placed in N KCl for 18 hours. HCl - hydrochloric acid.

The second titration curve, (See Figure III), obtained when the dialized roots were reimmersed in the potassium chloride solution for 18 hours, was again a strong acid type curve. This would indicate that organic acids of the cell sap were not involved in the titration.

The titration curves for the undialized roots were entirely different for the 30 seconds as compared to the 18 hour immersion in the potassium chloride solution. The 30 second immersion is a strong acid type titration curve. This was interpreted by Williams and Coleman (51) as evidence of exchangeable hydrogen on the external root surface. The titration curve for the 18 hour immersion in the potassium chloride is a buffered type curve. This is the type curve that would be expected if the cell sap acidity was entering into the reaction.

Nelly (33) studied the effect of electrodialysis on pea seeds at 80-150 volts, .4 amperes, and 24 °C. The most obvious result of electrodialysis of the seeds was a reduction in germination. Nelly concluded the effect on germination was caused by something other than the removal of electrolytes from the seeds. Loss of the power of germination was markedly reduced before any great amount of calcium, potassium or magnesium was removed. Nelly observed a greater quantity of bases than acids removed from the seeds during dialysis, and postulated that the cations were either adsorbed on the surface of the protoplasm or were in combination with anions which could not pass thru the cell membranes.

Seifriz (44) studied the effect of passing an electric current thru fruit and vegetable tissue. He observed a breakdown of the tissue at the cathode to a dark brown to black mass with a uniform pH of 12.2. No such reaction occurred when the tissue was placed at the anode. He attributed the cause of degeneration to breakdown of the protein by enzymes rendered active by the reducing conditions of the cathode.

Factors Affecting the Exchange Capacity of Plant Roots

The effects of freezing, boiling and of potassium chloride solution, were observed on the total titratable acidity of sweet pea roots. The roots were washed in distilled water, blotted dry, and five gram samples weighed out into 400 milliliter beakers and covered with 200 milliliters of normal potassium chloride or distilled water and frozen or boiled according to the treatment (See Table 2). Ten milliliters of .02 normal sodium hydroxide was then pipetted into each beaker and allowed to stand overnight and then the pH of each solution was recorded.

The lowest pH was recorded for the roots frozen in the potassium chloride solution. This might be explained by an increase in permeability of the roots due to a disorganization of the cytoplasm in the freezing and thawing process. The increase in acidity over the roots frozen in water would be due to the displacement of adsorbed hydrogen of the roots by the potassium from the solution. The efficiency of potassium in displacing the hydrogen from the root colloids can be seen from the high pH of the roots which were washed with potassium chloride after being frozen and thawed in the potassium chloride solution.

Boiling the roots reduced the amount of acidity in the supernatent solution when compared to frozen and unfrozen roots. This might be due to the effect of boiling on the permeability of the cells, upon coagulation of the proteins, or on the chemical composition of the root colloids. Boiling could also reduce the measured acidity by driving off volatile compounds such as carbonic acid.

Roots of sweet peas were dialized and oven-dried at 70°C. and then immersed in normal potassium chloride solution. After 48 hours, the roots failed to show any measureable exchange capacity. This would indicate the permeability of the root colloids had been destroyed in drying. Mattson (29) was able to determine the exchange capacity of dried roots by finely grinding the tissue and employing serial titrations.

Sources of Error in Determination of the Exchange Capacity

Differences in physiological maturity of the roots cause variations in the measured exchange capacities. Williams and Coleman (51) were able to show the highest rate of exchange for the tip portions of bean and corn roots. This would be the region in which the epidermis was least

TABLE 2

FACTORS AFFECTING THE EXCHANGEABLE ACIDITY OF SWEET PEA ROOTS AS MEASURED BY THE pH OF THE SOLUTION 21 HOURS AFTER 10 MILLILITERS OF .02 N NaOH WAS ADDED

Treatment*	Supernatent Liquid	pH
1. Untreated roots	N KCl	7.33
2. Frozen	N KCl	6.66
3. Frozen and washed with the KCl	N KCl	9.56
4. Frozen	H_2O	7.48
5. Boiled	N KCl	9.32
6. Boiled and washed with the KCl	N KCl	9.70

*All samples were 5 grams fresh weight and in 200 milliliters of supernatent liquid.

developed and the intra-cellular spaces were most accessible for entrance of ions from the external solution.

Sweet pea roots were harvested from nutrient solution cultures after one month and cut into three portions consisting of the lower, middle, and upper regions of the root system. The exchange capacity was determined for the three regions for both the dialized and undialized roots. The exchange capacity of the dialized roots was determined by the method described previously. The undialized roots were washed, placed in normal potassium chloride, and an excess of sodium hydroxide added. The solution was back titrated after 24 hours. Results are shown in Table 3.

TABLE 3

THE EXCHANGE CAPACITY OF DIFFERENT PORTIONS OF THE ROOT SYSTEM OF SWEET PEA WHICH DIFFERED IN PHYSIOLOGICAL MATURITY

Distance From Root Tip in Inches	Dialized*	Undialized*
0-3	39.86	426.0
3-4	34.38	367.0
6-9	28.95	268.0

*Expressed as milliequivalents / 100 grams of dry weight.

Although both dialized and undialized roots showed the same trend for an increase in the exchange capacity for the region nearest the growing tip, the difference was accentuated more by the undialized roots. This might be taken as further evidence that dialysis increases the permeability of the roots by disrupting the cytoplasm of the cells of the cortex which resulted in loss of the cell sap. The decrease in the exchange capacity of the more mature regions might then be due to the difference in the content of exchange material per unit of dry weight between mature and immature cells. The more mature regions of the root system could be expected to have a greater dry weight per unit of fresh weight which would tend to decrease the measured exchange capacity of the more mature regions of the root compared to the regions nearer the growing tip.

Another source of error encountered was a breakdown of the root tissue during dialysis similar to that reported by Seifriz (44). The roots became brown and discolored and caused a basic pH reading when placed in the potassium chloride solution. No answer has been found as to why this only occurred in some dialyses. Two separate crops of stock variety Shasta gave alkaline pH readings from all treatments. In other crops certain runs occurred in which part of the roots nearest to the cathode were discolored and basic in reaction.

The Exchange Capacity of Frozen Roots

Roots of sweet peas were frozen and stored for one year. The exchange capacity was determined along with freshly harvested sweet pea roots. A value of 42.0 milliequivalents per 100 grams was obtained for the frozen roots, and 37.41 milliequivalents per 100 grams for freshly harvested roots.

An attempt was made to displace the adsorbed cations of the plant root colloids by the mass action of hydrogen ions instead of the usual dialysis. The roots were frozen, then thawed in 200 milliliters of distilled weter to which 5 milliliters of normal hydrochloric acid was added and allowed to stand with occasional stirring thirty minutes. The roots were then washed in distilled water, centrifuged, and placed in normal potassium chloride solution. Exchange capacities of 51.3, 50.2, and 28.3 milliequivalents per 100 grams were obtained for stock, sweet peas, and snapdragon respectively.

RESULTS

The Cation Exchange Capacity of Plant Roots

The relative cation exchange capacities of the roots of a number of floriculture crops were determined at the University of Massachusetts. Additional values were determined at Michigan State College (See Table 4).

The exchange capacities of different plant species ranged from a high of 101.87 milliequivalents per 100 grams of dry tissue for the roots of annual larkspur to a low of 19.30 milliequivalents for snapdragon variety Sunray.

Not enough species were represented in the group to make generalizations about the exchange capacity of different plant families. However, the results obtained indicated that plants closely related botanically have similar exchange capacities. Different varieties of the same species showed similar exchange capacities and members of the same plant family had exchange capacities in the same range.

It was found that the substrate in which the plants were grown did not alter the relative exchange capacities of the plant roots as long as the physiological maturity of the root samples was comparable. When plants were grown in soil, gravel culture, water culture, and a mixture of sand and exchange resin, similar values for the exchange capacity of the roots were obtained for the same species.

TABLE 4

RELATIVE CATION EXCHANGE CAPACITY OF PLANT ROOTS OF DIFFERENT PLANT SPECIES

Plant	Variety	Culture	Cation Exchange Capacity[1]
Delphinium ajacis	Blue	resin	101.87
	Blue	soil	94.35[2]
	Blue	water	88.05
Mathiola incana annua	Lilac Lavender	soil	58.08[2]
	Lavender	water	44.51
Chrysanthemum hortorum	Indianapolis Pink	water	45.22
	Mefo	water	43.20
	Courtier	gravel	40.73[2]
Callistephus chinensis	Queen of Mkt.,Azure	water	44.23
Limonium sinuatum	Market Growers Blue	soil	44.63[2]
Lathyrus odoratus	Cuthbertson Mix.	gravel	42.76[2]
	Cuthbertson Mix.	water	39.86
	Cuthbertson Mix.	resin	35.46
Lupinus polyphyllus	Russel Hybrid	sand	40.51[2]
Gladiolus hybrida	Capeheart	gravel	38.90[2]
Narcissus tazetta	Paper White	gravel	37.05[2]
	Paper White	soil	27.48[2]
Rosa hybrida	Better Times	water	34.89
Lilium longiflorum	Croft	gravel	30.54[2]
	Croft	water	29.61
Pelargonium domesticum		soil	32.60
Pelargonium hortorum	Wallingford	gravel	29.23[2]
Dianthus caryophyllus	King Cardinal	water-gravel	31.34
	Northland		24.29[2]
Zea mays	Golden Cross Bantam	water	28.79
Antirrhinum majus	Skyscraper Alaska	gravel	26.69[2]
	Sunray	gravel	19.30[2]
	Spartan Rose	water	40.02
	Spartan Rose	water	25.24
	Spartan Rose	resin	26.13

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[1] Exchange capacities are expressed as milliequivalents per 100 grams of dry tissue and all values are averages of two or more determinations.

[2] Data from experiments conducted at the University of Massachusetts.

Water culture had the advantage that older roots, and a greater portion of the root system could be utilized in the determination of the exchange capacity than in the other methods of culture.

It was shown (See Table 3) that younger portions of the root system nearest the growing tip had a higher cation exchange capacity than portions farther back from the growing tip whose cells were more mature. This may have been due to a difference in permeability of the root cells of different regions of the root or it may have been due to diferences in dry weight of the cell walls per unit of exchange material associated with the cells. Where values for the exchange capacity of the roots from various methods of culture were not in agreement, it was felt that the difference could be explained by visible differences in the maturity of the root samples.

One discrepancy for which no explanation is offered was the difference in the exchange capacity obtained for the snapdragon variety Spartan Rose grown in water culture with two crops.

An attempt was made to determine the effect of various ion ratios and salt concentrations in the nutrient solution on the relative exchange capacity of the plant roots. The results proved variable (See Table 5). The different nutrient solutions employed had various effects on the growth of the plant roots of the different crops.

TABLE 5

THE EFFECT OF VARIOUS NUTRIENT SOLUTIONS ON THE RELATIVE CATION EXCHANGE CAPACITY OF PLANT ROOTS

(Expressed as milliequivalents/100 grams dry tissue)[1]

Plant	Low Ca Low K	Low Ca High K	Standard Hoagland	High Ca Low K	High Ca High K	2 X Hoagland
Larkspur	83.55	93.42	83.55	23.96	83.86	95.86
Stock	46.53	43.44	42.33		43.82	45.73
Chrysanthemum[3]	30.51	43.62	38.19	39.58	47.34	39.92
Snapdragon	18.15	24.26	23.64	16.07	28.60	24.99
Snapdragon					38.66	41.39
Corn	29.96	26.45	21.41	29.96	20.32	29.68

Plant	1/3 X Hoagland	Low Ca High K	Standard Hoagland	High Ca Low K	I.A.A.[2]	2 X Hoagland
Chrysanthemum[4]	40.86	31.99	46.72	46.10	40.79	47.56
Corn	28.62	23.40	33.61	39.58	29.68	32.75
China Aster	42.45	45.24	47.93	14.78		43.12

[1] All values are averages of two or more determinations.

[2] Plant tops were sprayed weekly with 1000 p.p.m. of indoleacetic acid.

[3] Variety White Mefo.

[4] Variety Indianapolis Pink.

Two solutions in particular had an adverse effect on the growth of several plant species. One of these was the low calcium : low potassium solution in which the pH decreased to between 3 and 4 as the plants grew. The roots of many species grown in this solution developed a coarse texture not found in the roots of plants in the other solutions (See Figure IV). The coarseness was caused in part by the development of short, stubby, branch roots which seemed to be accompanied by a breakdown of the root tip.

The other solution which had an adverse effect on the root growth of many species was the high calcium: low potassium solution. Most plants made noticeably less root growth in this solution compared to the other solutions. Low exchange capacities were obtained from roots in this treatment for some plants (See Table 5). It was noted that when this was the case, the pH of the supernatent liquid was higher than for roots from the other treatments when the dialized roots were placed in the potassium chloride solution. This might indicate that the cations were not easily removed from the roots in the dialysis process when the roots had a high percentage saturation of adsorbed calcium ions. This hypothesis might be strengthened by the fact that stock, a crop which showed a high calcium absorption, gave the most difficulty in determining root exchange capacity. However, it is not felt that from these long term

Figure IV

Differences in the growth and texture of corn roots in nutrient solutions with different pH and calcium concentrations. Left to right: low Ca:low K, pH 3.52; standard Hoagland, pH 7.02; standard Hoagland with NH_4, pH 3.29.

experiments it is possible to differentiate between the effects of the organic composition of the roots and the nature of the adsorbed cations in regard to their effect upon the cation exchange capacity of the roots.

The Effect of the Different Nutrient Solutions on the Plant Growth and Chemical Composition of the Plant Tops

Corn variety Golden Cross Bantam. The results of chemical analyses of tops of corn plants grown in various nutrient solutions showed that in comparison with the other plants used in the experiment, young corn plants contained high percentages of potassium but low percentages of calcium (See Table 6). The calcium and potassium content of the tops of corn plants was related to the concentrations of the respective ions in the nutrient solution. However, high concentrations of potassium in the nutrient solution lowered the calcium content in the plant tops, while high concentrations of calcium in the nutrient solution had little effect on the potassium content of the tops (3). Of interest was the increase in the potassium content of corn plants which were sprayed weekly with 1000 parts per million of indoleacetic acid over those which were unsprayed when both were grown in standard Hoagland solution.

In contrast to potassium and calcium, the magnesium concentration was constant in all solutions except the one-third and 3 X Hoagland solutions. Differences in magnesium

TABLE 6

THE GROWTH AS MEASURED BY DRY WEIGHT AND THE PERCENTAGE COMPOSITION OF CALCIUM, POTASSIUM, AND MAGNESIUM IN THE TOPS OF CORN VARIETY GOLDEN CROSS BANTAM GROWN IN VARIOUS NUTRIENT SOLUTIONS

(A. Into solution:February 1, 1954;harvested:March 23, 1954)

Treatment	Dry Weight*	Expressed as % Dry Weight %K	%Ca	%Mg
Low Ca:Low K	4.72	3.53	.22	.20
Low Ca:High K	5.20	6.91	.23	.27
1 Hoagland	3.59	5.29	.34	.33
High Ca:Low K	2.56	3.96	.63	.33
High Ca:High K	5.12	6.73	.33	.27
3 Hoagland	4.35	5.68	.46	.31
1 Hoagland NH_4	4.16	5.78	.21	.23
L.S.D. .05	1.44	1.15	.07	.03
L.S.D. .01	2.02	1.61	.10	.04

(B. Into solution:August 6, 1953; harvested:August 20, 1953)

Treatment	Dry Weight*	Expressed as % Dry Weight %K	%Ca	%Mg
1/3 Hoagland	4.43	5.20	.36	.36
1 Hoagland	3.96	6.98	.29	.25
3 Hoagland	3.20	5.53	.29	.29
High Ca:Low K	2.90	1.69	.38	.36
Low Ca:High K	3.90	3.49	.27	.39
1 Hoagland I.A.A.	4.01	8.63	.27	.26
L.S.D. .05	.74	1.00	.05	.03
L.S.D. .01	1.04	1.43	.07	.04

*Average dry weight of three plants in grams.

content of plant tops in the different treatments can be ascribed to the different potassium:calcium concentrations in the nutrient solutions. Increased concentrations of potassium in the nutrient solutions decreased the magnesium content of the tops of corn plants. The concentration of calcium in the nutrient solution had little effect on the absorption of magnesium by corn.

Corn plants grown in different nutrient solutions with different concentrations of potassium, produced more growth as measured by the dry weight of the tops in the solutions with the higher potassium concentrations. This was especially noticeable in the crop grown in the winter and indicates a high potassium requirement for corn.

<u>Snapdragon variety Spartan Rose</u>. The results of chemical analyses of tops of snapdragon plants grown in various nutrient solutions indicated that the content of potassium and calcium in the plant tissue in the different treatments was remarkably constant (See Table 7). This would indicate that the maximum potassium and calcium content for snapdragon was approached by plants grown in the standard Hoagland solution.

High concentrations of potassium in the nutrient solution lowered the calcium content of snapdragon. The calcium concentration in the nutrient solution had little effect on the potassium content of the plant tissue.

TABLE 7

THE GROWTH AS MEASURED BY DRY WEIGHT AND THE PERCENTAGE COMPOSITION OF CALCIUM, POTASSIUM, AND MAGNESIUM IN THE TOPS OF SNAPDRAGON VARIETY SPARTAN ROSE GROWN IN VARIOUS NUTRIENT SOLUTIONS

(A. Into solution:September 18, 1953;harvested:October 29,1953)

Treatment	Dry Weight*	Expressed as % Dry Weight %K	 %Ca	 %Mg
Low Ca:Low K	3.85	1.49	.33	.40
Low Ca:High K	5.69	5.55	.41	.57
1 Hoagland	5.35	4.89	1.10	.66
High Ca:Low K	5.24	2.47	1.63	.72
High Ca:High K	5.33	5.69	.76	.40
2 Hoagland	3.69	4.99	1.13	.66
L.S.D. .05	1.39	.76	.10	.05
L.S.D. .01	1.88	1.08	.14	.08

(B. Into solution:February 18, 1954;harvested:April 10, 1954)

Treatment	Dry Weight*	Expressed as % Dry Weight %K	 %Ca	 %Mg
Low Ca:Low K	3.09	1.93	.44	.47
Low Ca:High K	4.00	4.83	.47	.52
1 Hoagland	7.53	3.50	.90	.53
High Ca:Low K	6.13	2.10	1.56	.55
High Ca:High K	8.62	4.33	.81	.44
2 Hoagland	8.34	3.75	1.02	.43
1 Hoagland NH_4	4.63	2.77	.88	.47
L.S.D. .05	N.S.	.75	.29	.13
L.S.D. .01		1.14	.44	.20

*Average dry weight of three plants in grams.

The growth of snapdragon as measured by dry weight of the tops showed relatively little difference with wide calcium and potassium ratios in the nutrient solutions. This also indicated that the potassium and calcium contents determined in the plant tissue were near the maximum values, and the requirement of snapdragon for potassium and calcium was relatively low.

The tissue in the tops of snapdragon plants had the highest magnesium content of any of the plant species studied. The content of magnesium in the plant tops showed a significant decrease when the concentration of potassium ions in the nutrient solution was increased. The concentration of calcium ions in the nutrient solution had little effect on the magnesium content of the plant tops.

Of all the plant species studied, the growth of snapdragon plants was most seriously affected by a decrease in the solution pH. The critical pH of the nutrient solution for snapdragon plants was near 4. When the pH of the solution fell below 4, the plants wilted and a breakdown of the root tissue occurred.

<u>Chrysanthemum variety White Mefo</u>. The results of chemical analyses of tops of chrysanthemum plants grown in nutrient solutions indicated that chrysanthemums absorb large amounts of Potassium and moderate amounts of calcium when compared with the other plants studied (See Table 8).

TABLE 8

THE GROWTH AS MEASURED BY DRY WEIGHT AND THE PERCENTAGE COMPOSITION OF CALCIUM, POTASSIUM, AND MAGNESIUM IN THE TOPS OF CHRYSANTHEMUM VARIETY WHITE MEFO GROWN IN VARIOUS NUTRIENT SOLUTIONS

(Into solution:December 18, 1953; harvested:January 25, 1954)

Treatment	Dry Weight*	Expressed as % Dry Weight		
		%K	%Ca	%Mg
Low Ca:Low K	10.63	3.33	.54	.49
Low Ca:High K	10.99	7.66	.44	.40
1 Hoagland	13.89	5.47	.94	.43
High Ca:Low K	10.61	3.04	1.31	.44
High Ca:High K	12.11	7.13	.93	.37
3 Hoagland	10.04	5.73	.81	.34
1 Hoagland NH_4	13.90	4.93	.96	.39
L.S.D. .05	1.76	1.03	.18	.06
L.S.D. .01	2.45	1.46	.26	.09

*Average dry weight of three plants in grams.

Increased concentrations of potassium ions in the nutrient solutions decreased the calcium content in the tops of chrysanthemum plants. The concentration of calcium in the nutrient solution had little effect on the potassium content of chrysanthemum tops.

The growth of chrysanthemum plants in the different nutrient solutions as measured by dry weight of tops indicated that chrysanthemums had a high requirement for both potassium and calcium (2).

The magnesium content in the tops of chrysanthemum showed a reverse relationship with the concentration of potassium and calcium ions in the nutrient solution. Increasing concentrations of potassium and calcium ions in the nutrient solution caused a decrease in the magnesium content of the plant tops. The concentration of potassium in the nutrient solution had a greater depressive effect on magnesium absorption by the roots of chrysanthemum plants than did the concentration of calcium.

Chrysanthemum was one of the more tolerant species in regard to the effect of pH of the nutrient solution on growth and cation absorption. A slight, although not significant decrease of potassium and magnesium content in the plant tops could be attributed to a decrease in the solution pH.

Stock varieties Shasta and Lavender. The results of chemical analyses of the tops of stock plants grown in nutrient solutions indicated that the plant tissue contained high percentages of both calcium and potassium and especially when the concentrations of these ions were high in the nutrient solutions (37). Compared to the other plant species studied, stock contained a high percentage of calcium in the plant tissue (See Table 9).

A high concentration of potassium ions in the nutrient solution decreased the calcium content of the tops of stock slightly, compared to plants grown at a lower potassium level. However, the potassium concentration in the nutrient solution had less effect on the calcium content of stock plants than it did with the other plant species analyzed. With the variety Shasta, an increase in concentration of calcium in the nutrient solution increased the potassium content of the plant tops. With the variety Lavender, an increase in the calcium concentration in the nutrient solution caused a decrease in the potassium concentration of the tops. Not enough different concentrations of potassium and calcium were available in the nutrient solutions to observe the full trend of the effect of concentration of calcium in the nutrient solution on potassium absorption. However, it appeared that at low concentrations of calcium in the nutrient solution an increase in calcium concentration

TABLE 9

THE GROWTH AS MEASURED BY DRY WEIGHT AND THE PERCENTAGE COMPOSITION OF CALCIUM, POTASSIUM, AND MAGNESIUM IN THE TOPS OF STOCK VARIETIES SHASTA AND LAVENDER GROWN IN VARIOUS NUTRIENT SOLUTIONS

(A. Variety Shasta)
(Into solution:December 18, 1953;harvested:January 29, 1954)

Treatment	Dry Weight*	Expressed as % Dry Weight		
		%K	%Ca	%Mg
Low Ca:Low K	4.73	2.39	.48	.33
Low Ca:High K	4.51	5.56	.71	.43
1 Hoagland	3.90	4.86	1.90	.32
High Ca:Low K	4.85	2.36	2.08	.28
High Ca:High K	3.76	6.70	1.89	.27
3 Hoagland	3.42	7.48	2.17	.31
L.S.D. .05	1.36	.35	.48	.06
L.S.D. .01	1.89	.49	.67	.08

(B. Variety Lavender)
(Into solution:November 14, 1953;harvested:December 31, 1953)

Treatment	Dry Weight*	Expressed as % Dry Weight		
		%K	%Ca	%Mg
Low Ca:Low K	5.05	2.64	.68	.35
Low Ca:High K	5.19	7.32	.86	.49
1 Hoagland	4.88	5.32	2.01	.34
High Ca:Low K	4.44	2.96	2.35	.30
High Ca:High K	5.14	6.10	1.98	.29
3 Hoagland	3.28	6.19	2.35	.36
L.S.D. .05	1.23	.49	.15	.01
L.S.D. .01	1.70	.69	.20	.02

*Average dry weight of three plants in grams.

might stimulate potassium absorption, while at very high concentrations a further increase might cause a decrease in the potassium absorption by stock plants (35).

The content of magnesium in the tissue of stock plants was affected more by the concentration of calcium in the nutrient solution than by the concentration of potassium. High levels of calcium in the nutrient solution decreased the absorption of magnesium by stock plants. In solutions where the concentration of calcium was low and the concentration of potassium high, the magnesium content of the tops was increased.

The growth of stock plants as measured by dry weight of the plant tops in nutrient solution with different calcium and potassium concentrations was quite constant. This indicates that although stock plants contain high percentages of calcium and potassium, the actual requirement for these elements is not as great as in chrysanthemum.

Larkspur variety Light Blue. The results of chemical analyses of the tops of annual larkspur plants showed that larkspur contained a high percentage of potassium compared to calcium (See Table 10). In this respect the composition of larkspur was much more like chrysanthemum than it was like stock. The greatest amount of dry weight was produced when plants were grown in the standard Hoagland solution, and the high calcium:high potassium solutions where there was a balance between calcium and potassium ions in the substrate.

TABLE 10

THE GROWTH AS MEASURED BY DRY WEIGHT AND THE PERCENTAGE COMPOSITION OF CALCIUM, POTASSIUM AND MAGNESIUM IN THE TOPS OF LARKSPUR VARIETY LIGHT BLUE GROWN IN VARIOUS NUTRIENT SOLUTIONS

(Into solution: January 6, 1954; harvested: March 9, 1954)

Treatment	Dry Weight*	Expressed as % Dry Weight		
		%K	%Ca	%Mg
Low Ca:Low K	6.86	2.82	.56	.34
Low Ca:High K	4.47	6.86	.45	.32
1 Hoagland	7.55	5.16	.71	.30
High Ca:Low K	5.72	3.37	1.19	.29
High Ca:High K	8.25	5.53	.56	.23
2 Hoagland	4.66	6.26	.86	.29
1 Hoagland NH_4	5.66	4.66	.82	.28
L.S.D. .05	2.26	1.00	.55	.18
L.S.D. .01	3.17	1.40	.77	.25

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*Average dry weight of three plants in grams.

With increasing concentrations of potassium ions in the nutrient solutions, the percentage composition of calcium in the plant tops tended to decrease. This indicated that increasing concentrations of potassium ions in the substrate tended to interfere with the absorption of calcium . An increase in the concentration of calcium ions in the nutrient solution failed to decrease the potassium content of the tops of larkspur plants. In fact, the plants grown in the high calcium:low potassium had a higher potassium content that the plants grown in the low calcium:low potassium solution. Since the low calcium:low potassium solution had ammonium ions present, and the high calcium:low potassium solution did not, the difference in potassium content in the plant tops might be attributed to an interference of ammonium and hydrogen ions with absorption of potassium ions from the nutrient solution by larkspur roots.

The magnesium content of the tops of larkspur plants was affected by the concentration of both calcium and potassium ions in the nutrient solution. High levels of potassium and calcium in the nutrient solution decreased the content of magnesium in the tops of larkspur. The concentration of calcium ions in the solution had a slightly greater, although not significant effect on magnesium content of larkspur than did the concentration of potassium ions.

DISCUSSION

The Relationship Between Relative Cation Exchange Capacity of Plant Roots and Potassium Absorption

In order to show the relationship between cation exchange capacity of the root system and potassium absorption, the crops studied are listed in the order of increasing root exchange capacities and the treatments in the order of increasing potassium concentrations (See Table 11). The nutrient solution containing the highest concentration of calcium and the lowest concentration of potassium employed in the experiment was selected as a reference nutrient solution. The content of potassium in the plant tops grown in all other solutions was compared with the content of potassium in plants grown in the high calcium:low potassium solution, and the difference was expressed as milliequivalents of potassium lost or gained.

The maximum amount of potassium that a plant species may contain is a characteristic of the particular plant species (36). The percent of the maximum potassium content that a plant does contain is a measure of the plant's ability to absorb potassium under the environment in which the plant was grown.

Although plants with the lower root exchange capacities such as corn may have contained larger amounts of potassium than plants with higher root exchange capacities accumulated at lower potassium concentrations; at higher concentrations of potassium in the nutrient solution, the plants with higher root exchange capacities may take up as much or more potassium than plants with lower exchange capacities. This means that in terms of maximum potassium content, the plants with roots with a low cation exchange capacity were able to accumulate a greater percentage of their maximum potassium content at low concentrations of potassium in the nutrient solution than plants with a high cation exchange capacity. Plants with a high root exchange capacity, such as stock and chrysanthemum, which were able to accumulate relatively less potassium from low concentrations of potassium in the nutrient solution compared to plants with a low root exchange capacity, increased the most in potassium content when the concentration of potassium ions in the nutrient solution increased.

As a possible explanation for the observed potassium absorption by the different plant species, it is necessary to consider the activity of calcium and potassium ions in solution. In very dilute solutions the effective concentration, as calculated from ion activities, of equal molar concentrations of potassium and calcium salts are nearly equal (17). According to the theory of interionic attraction of Debye-Hückel (17), in dilute solutions an increase in molar concentration affects a greater reduction in the activity coefficient of divalent than monovalent ions. This would apply to the range of concentrations which were employed in the nutrient solutions of the experiment. Thus, as the molar concentrations of potassium and calcium increase in the nutrient solution, the disparity between the effective concentrations of potassium and calcium ions increases in favor of potassium.

From this it appears that the absorption of potassium by plants is related to the cation exchange capacity of the plant roots and the effective concentration of potassium ions in relation to other ions in the nutrient solution. Plants with higher root exchange capacities show greater increases in potassium content than plants with lower root exchange capacities as the effective concentration of potassium ions increases in respect to other ions in the nutrient solution.

TABLE 11

THE POTASSIUM CONTENT OF THE TOPS OF SOME PLANT SPECIES WITH DIFFERENT ROOT CATION EXCHANGE CAPACITIES GROWN IN NUTRIENT SOLUTIONS WITH INCREASING POTASSIUM CONCENTRATIONS

(A. Crops grown in fall and winter)

Crop[3]	[1]	Solutions [2]				
	Low K High Ca	Low K Low Ca	1 Hoagland	High K High Ca	3 Hoagland	High K Low Ca
Corn	1015	-110	+341	+711	+441	+766
Snapdragon	633	-251	+621	+826	+646	+790
Snapdragon	538	-69	+359	+572	+424	+700
Chrysanthemum	779	+75	+624	+1049	+690	+1185
Stock, Shasta	605	+8	+641	+1113	+1313	+821
Stock, Lav.	589	+88	+775	+975	+998	+1288
Larkspur	864	-141	+459	+554	+741	+895

(B. Crops grown in spring and summer)

Crop[3]	1/3 Hoagland[1]	Solutions [2]		
		1 Hoagland	2 Hoagland	High K Low Ca
Corn	1333	+457	+85	-438
Snapdragon	949	0	+13	+243
China Aster	1090	+195	+359	+428
Stock, Shasta	767	+464	+769	+1310

[1] Milliequivalents of potassium/1000 grams dry weight.

[2] Milliequivalents of potassium/1000 grams dry weight lost or gained compared to the high Ca:Low K solution.

[3] Plant species are arranged in the order of increasing root cation exchange capacities.

The Relationship Between Relative Cation Exchange Capacity of Plant Roots and Calcium Absorption

The relationship between cation exchange capacity of plant roots and calcium absorption by different crops is less apparent than with potassium or magnesium absorption. Greatest increases in calcium content with increasing calcium concentrations in the nutrient solution were registered by stock, snapdragon, chrysanthemum, larkspur, and corn in that order (See Table 12). This does not follow the order of root exchange capacities but rather the order of decreasing calcium content.

If equilibrium between the calcium ions within the plant and those in the external solution were a limiting factor in ion accumulation (1), then plants which tended to remove the most calcium from the internal solution would also tend to absorb the most calcium from the external nutrient solution. Plants such as corn, chrysanthemum, and larkspur, which contain relatively less calcium than stock and snapdragon, would reach equilibrium with the external solution at a lower calcium content and would show less gain in calcium content with an increase in the calcium concentration of the nutrient solution. This in no way contradicts the hypothesis that root exchange capacity is a factor in cation absorption, but rather that in long term experiments with nutrient solutions such as were employed, the effect of root exchange capacity on calcium absorption is overshadowed by the utilization of calcium within the plant.

TABLE 12

THE CALCIUM CONTENT OF THE TOPS OF SOME PLANT SPECIES WITH DIFFERENT ROOT CATION EXCHANGE CAPACITIES GROWN IN NUTRIENT SOLUTIONS WITH INCREASING CALCIUM CONCENTRATIONS

(A. Crops grown fall and winter)

Crop[3]	Low Ca High K[1]	Solutions[2]				
		Low Ca Low K	1 Hoagland	High Ca High K	3 Hoagland	High Ca Low K
Corn	115	-5	+55	+50	+115	+100
Snapdragon	205	-40	+345	+175	+360	+610
Snapdragon	235	-15	+215	+170	+275	+545
Chrysanthemum	220	+50	+250	+245	+185	+445
Stock, Shasta	355	-115	+595	+590	+730	+685
Stock, Lav.	430	-90	+575	+560	+745	+745
Larkspur	225	+55	+130	+155	+205	+370

(B. Crops grown in spring and summer)

Crop[3]	Low Ca High K	Solutions[2]			
		1/2 Hoagland	1 Hoagland	2 Hoagland	High Ca Low K
Corn	135	+45	+10	+10	+55
Snapdragon	130	+280	+280	+300	+580
China Aster	85	+230	+205	+235	+565
Stock	215	+200	+615	+710	+1090

[1] Milliequivalents of calcium/1000 grams of dry weight.

[2] Milliequivalents of calcium/1000 grams of dry weight lost or gained compared to the low Ca:high K solution.

[3] Plant species are arranged in the order of increasing root cation exchange capacities.

The results obtained in nutrient solutions with calcium are not necessarily the same as those which would be obtained in soil. It is possible to maintain much higher concentrations of soluble calcium in nutrient solutions than is possible in soil, and this would affect calcium absorption by plants. Also as Wadleigh and Bower (50) have pointed out, calcium is held more strongly by the clay colloids in the soil than are monovalent ions and this introduces the difference between calcium absorption by plants from soil as compared to water culture.

The Relationship Between Relative Cation Exchange Capacity of Plant Roots and Magnesium Absorption

The same concentration of magnesium ions was employed in all nutrient solutions. Thus, the difference in absorption of magnesium by the different plants can be attributed to the effects of varying calcium and potassium concentrations in the nutrient solutions. The plants studied are listed in the order of increasing cation exchange capacities of the roots and the gain or loss in milliequivalents of magnesium in the plant tops compared to plants grown in standard Hoagland solution is given in Table 13.

At low levels of both calcium and potassium in the nutrient solution, the tops of plants whose roots had high relative cation exchange capacities tended to contain more magnesium than when the plants were grown in standard Hoagland solution. This would be in agreement with the hypothesis that plants with high root exchange capacity tend to show the greatest increase in absorption of the ion which is present in the highest effective concentration in the nutrient solution. Plants with low root exchange capacities showed a decrease in magnesium content of the tops when the concentration of both calcium and potassium was lower than in the standard Hoagland solution. Since the pH of this solution was low, this could have been a factor in magnesium absorption with snapdragon and corn.

Corn, Snapdragon, and chrysanthemum plants decreased in the percentage of magnesium in the plant tops when the concentration of potassium was increased and the concentration of calcium decreased in the solution compared to the plants grown in the standard Hoagland solution. In contrast, the tops of stock and larkspur increased in magnesium content under the same conditions compared to plants grown in standard Hoagland solution. The content of magnesium in the plant tops for the same species appeared to be affected just opposite when the calcium concentration was increased and the potassium concentration decreased in the nutrient solution. Stock and larkspur decreased in magnesium content, while corn, snapdragon, and chrysanthemum were less affected when compared to plants grown in the standard Hoagland solution.

TABLE 13

THE MAGNESIUM CONTENT OF THE TOPS OF SOME PLANT SPECIES WITH DIFFERENT ROOT CATION EXCHANGE CAPACITIES GROWN IN NUTRIENT SOLUTIONS WITH DIFFERENT CONCENTRATIONS OF CALCIUM AND POTASSIUM

Crop[3]	1 Hoagland	Solutions[2]		
		Low Ca Low K	High K Low Ca	High Ca Low K
Corn	275	-108	-50	0
Snapdragon	550	-216	-75	+50
Snapdragon	458	-66	-25	-16
Chrysanthemum	358	+50	-25	+8
Stock, Shasta	266	+8	+91	-33
Stock, Lav.	283	+8	+125	-8
Larkspur	250	+33	+16	-8

[1] Milliequivalents of magnesium/1000 grams of dry weight.

[2] Milliequivalents of magnesium/1000 grams of dry weight lost or gained compared to the 1 Hoagland solution.

[3] Plant species are arranged in the order of increasing root cation exchange capacities.

It appears that for plants studied, the calcium ions depress the absorption of magnesium ions in plants with high root exchange capacities, especially those that contain large amounts of calcium in the tops. Potassium ions depressed the absorption of magnesium ions in plants with low root exchange capacities and in those plants which contained large amounts of potassium in the plant tops. This would suggest that the content of magnesium in the plant species studied was influenced by the cation balance in the plants (4). Excessive absorption of either calcium or potassium caused a decrease in magnesium content.

Determination of the Relative Cation Exchange Capacities of Plant Roots

Two theoretical considerations are involved in regard to the determination of the relative cation exchange capacities of plant roots. What is actually being measured in the determination? Why are there differences in the exchange capacities of the roots of different plant species?

Roberts et al (39) found that in apple leaves pectinaceous compounds form a continuous pathway reaching from the outside of the leaf and extending to the walls of the vein extensions. Similar pathways probably are present in plant roots. Broyer (5) concluded that ions moved along continuous protoplasmic paths to the xylem, especially when the concentration of salts in the external solution was high.

Frey-Wyssling (15) observed that cellulosic cell walls are permeable to all plasmolytic agents and therefore to nutrient ions. Thus both cellulose compounds in the cell walls and pectinaceous compounds in the cell walls and intracellular spaces may enter into the measured cation exchange capacity of the plant roots. The comparison of the exchange capacities and titration curves of dialized and undialized roots (See Figure III) indicated that the permeability of cytoplasm in the cells had been increased by electrodialysis. There is also a possibility that the cytoplasm of the plant cells enters into the measured exchange reaction. Mattson (28), however, feels that the cell wall is more important in this respect than the cytoplasm.

It is felt that with plasmolysis of cells and disorganization of cytoplasm brought about by dialysis, the resulting increase in permeability of the root tissues allows all of the cortical cells to enter into the measured exchange reaction (19, 38). The fact that as a rule coarser rooted species tend to have higher exchange capacities than fine-rooted species, would be explained by this assumption. This does not mean that the chemical composition of the exchange materials in different plant species does not influence the measured exchange capacity. To account for the differences in the exchange capacities of the roots of different plant species, it is assumed that there are differences in the amounts and chemical composition of colloidal material in the cell walls, in the intracellular spaces, and in cytoplasm of the cortical cells of the plant roots. However, the ratio of different tissues in the root should be kept in mind in evaluating the relative measured exchange capacity of different plants. From the texture of the roots, corn should behave as if the root exchange capacity were lower than that actually measured when compared with finer rooted crops. Comparing snapdragon and stock with coarser rooted species, they should behave as if their exchange capacities were higher than those actually measured. It is felt that the nutrient composition of these crops tends to show that they do behave in this way.

Hayward (18) has shown that composition of the nutrient solution can affect the ratio of the quantities of the different tissues in plant roots. This may account in part for differences in the root exchange capacities which were obtained in the different nutrient treatments.

Other factors besides those mentioned can also affect the interpretation of root exchange capacity data. McLean and Baker (31) point out that exchange capacity is no measure of bonding energy for a particular cation. Plant colloids with the same exchange capacity may have different bonding energies for specific cations and this will alter ion absorption ratios.

Practical Applications

The interpretation of relative root exchange capacity values in terms of practical applications for predicting the cation needs of plants in soil is difficult. Other factors besides root exchange capacity determine the amount of a particular fertilizer element needed in the soil (32). The extent of the root system and the texture of the roots, influence the ability of a plant to absorb mineral cations from the soil as well as the root exchange capacity. The actual requirement for a particular cation in the metabolic processes of a plant species does not appear to be related to the root exchange capacity of the plant. Additional information is therefore necessary about the nutrient requirements of the plant in all of the different physiological stages of development and under different seasonal conditions of light, moisture, and temperature before a fertilizer program for a crop can be derived. After plant nutrient requirements are known, along with the amount already available in the soil, the ability of the plant to absorb specific cations can be considered (11, 12, 26, 36). A fertilizer program can then be adopted which attempts to alter the existing ratios of the different cations in the soil for best plant growth (45, 48).

Although the data obtained in the experiment conducted, tends to show the effect of root exchange capacity on ion absorption, some interpretations can be made from growth responses in the different solutions in regard to requirements of the crops studied for the cations determined.

Some general observations were also made of the texture and extent of the root systems of the different plant species grown in nutrient solutions. On the basis of these observations, interpretations of nutrient requirements , and literature reviewed (2, 3, 11, 12, 14, 26, 32, 36, 37, 46, 48), an attempt was made to predict the relative potassium levels needed in soil for the plants studied (See Table 14). Each species was given a numerical rating between one and three on the basis of its potassium need for the item considered. For example, corn has a relatively low root exchange capacity so that it tends to absorb potassium easily from low concentrations of potassium. It was given a relative value of one for potassium need on the basis of exchange capacity. Larkspur with a high exchange capacity was given a relative value of three for the same item. Considering all of the plant characteristics listed as of equal value in determining the potassium need of the plant in the soil, the plant species are listed in the order of their decreasing need for available potassium in the soil: chrysanthemum, stock, corn, larkspur, and snapdragon (See Table 14). This does not mean that chrysanthemum would remove more potassium from the soil than corn, but rather that in orderto obtain the potassium necessary for the best growth, chrysanthemum needs a higher level of readily available potassium in the soil than corn.

TABLE 14

A RELATIVE EVALUATION OF THE AVAILABLE POTASSIUM NEEDED IN SOIL BY THE PLANT SPECIES STUDIED ON THE BASIS OF SPECIES CHARACTERISTICS

Species Characteristics	Plant Species				
	Corn	Snapdragon	Chrysanthemum	Stock	Larkspur
Cation exchange capacity	1	1	2	2	3
Potassium requirement	3	1	3	2	1
Extent of root system	1	2	2	3	2
Texture of roots	3	2	3	1	2
Salt tolerance	2	1	3	3	1
Total*	10	7	13	11	9

*The higher the number the higher the level of available potassium needed.

SUMMARY

The relative cation exchange capacities were determined for the roots of a number of floriculture crops. The majority of the species studied had relative root cation exchange capacities between 25 and 45 milliequivalents of cations per 100 grams dry weight of roots. Annual larkspur, however, had an exchange capacity of 94 milliequivalents per 100 grams of dry weight. The cation exchange capacity of the roots of plants which were closely related botanically tended to be similar. Evidence was presented to show that the exchange capacity was possibly associated with cells of the cortex of the root. It was not determined whether the site of the measured exchange capacity was in the cell wall or the cytoplasm.

In addition to the root exchange capacity, the calcium, magnesium, and potassium content of the top portions of annual larkspur, stock, chrysanthemum, snapdragon, and corn grown in different nutrient solutions was determined on a flame spectrophotometer. The content of potassium in the plant tops was found to be related to the concentration of potassium ions in the nutrient solution and the particular plant species. When plants were grown in standard Hoagland solution during the winter, all species contained near 1200 milliequivalents per 1000 grams of dry tissue. The different

species grown in spring and summer in standard Hoagland solution showed more variation in potassium content (see Table 11). The growth of plants in the different nutrient solutions indicated a higher potassium requirement in winter than in spring and summer. Corn and chrysanthemum had the highest potassium requirements of the crops grown. The concentration of calcium in the nutrient solution had little effect on the concentration of potassium in the plant tops.

The content of calcium in the plant tops was affected by the concentration of calcium ions in the nutrient solution and the particular plant species involved. However, in addition, the concentration of potassium ions in the nutrient solution had an effect upon the calcium content of the plant tops. An increase in the concentration of potassium ions in the nutrient solution tended to decrease the calcium content in the tops of all plants. Potassium ions had less effect upon calcium absorption by stock, however, than with other crops. Stock also had the highest calcium content of the species studied (See Table 12).

The different plant species studied had varying amounts of magnesium in the plant tops when grown in standard Hoagland solution. Snapdragon contained the most magnesium (550 milliequivalents per 1000 grams of dry tissue), and larkspur contained the least (250 milliequivalents per 1000 grams of dry tissue).

The absorption of magnesium as measured by the concentration in the plant tops was affected by both the concentration of potassium and calcium ions in the nutrient solution. The magnesium content in the tops of corn, snapdragon, and chrysanthemum tended to be decreased most by increasing potassium concentrations in the nutrient solution, while the magnesium content of stock tended to be decreased most by increasing calcium concentrations in the nutrient solution. Larkspur showed little difference in the effect of either potassium or calcium concentration in the nutrient solution upon the magnesium content of the plant tops.

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