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The Influence of Age on the Cation Exchange Capacity of Plant Roots

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THE INFLUENCE OF AGE ON THE CATION EXCHANGE CAPACITY OF PLANT ROOTS

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INTRODUCTION AND REVIEW OF LITERATURE

A yellowing which develops in some plants growing on naturally calcareous soils is called lime-induced chlorosis. The problem is complex, as indicated by Brown and Holmes (1956) and Porter and Thorne (1955). Species and varieties of plants differ in their iron requirements, susceptibility to lime-induced chlorosis, and interacting soil factors which affect iron supply (Thorne et al. 1950). Chlorosis of plants does not appear, therefore, to stem from a common causative factor. At least a part of this difference has been found to be associated with the plant roots. Thus, through the use of a resistant root stock Wann (1941) was able to produce non-chlorotic grapes. These grapes grown under similar conditions without the resistant root stock would have been highly chlorotic. Certain citrus root stocks have also been used on calcareous soils because they give citrus trees resistance to chlorosis.

The physiological property or properties of plant roots that produce this difference is little understood. It is suggested that the dominant metal enzyme of the terminal oxidase could give this difference (Brown and Hendricks, 1952, and Brown, 1953). It has been found that plants known to be susceptible to lime-induced chlorosis had predominately an iron-containing enzyme as a terminal oxidase, whereas plants that failed to go chlorotic in high-lime soils had a copper-containing enzyme. Since iron is not at the deficiency level in the soils producing this chlorosis (Thorne and Peterson, 1954), a root

property other than the dominant oxidase enzyme must be operating.

Colloids, particularly pectins (Keller and Deuel, 1957), present in plant roots possess electrical charges, usually negative, which give them the ability to adsorb cations. It has been found that roots not only have a definite measurable capacity to adsorb cations, but that the values vary with species (Drake et al. 1950, Graham and Baker, 1951, Williams and Coleman, 1950, Marcour, 1954, and Smith, 1955), with environmental temperature (Williams and Coleman, 1950), and with nutrition (Huffaker and Wallace, 1959). This cation exchange capacity[a] is a definite property of the external portions of root surfaces since cation exchange is exhibited even in the absence of plant metabolism. Williams and Coleman (1950) obtained data that are nearly identical regardless of the condition of the roots. It seems likely that the negative charge possessed by the root surface is associated with non-living portions, or compounds which undergo no immediate change on the diminution or cessation of metabolism. It has been determined that roots ether killed (Williams and Coleman, 1950) or roots that are dried (Marcour, 1954) have the same CEC as live roots. Evidence presented by most of the workers previously cited strongly indicates that a surface phenomenon is under investigation. This is substantiated by the rapidity of the exchange reaction between plant roots and salt solutions, and the large amount of ions involved in the exchange.

The initial step of transferring nutrients from the growth medium to the root xylem involves an exchange of hydrogen, hydroxyl, or bicarbonate ions on the surface of the root for nutrient ions of the substrate (Overstreet and Dean, 1951, and Overstreet and Jacobson,

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a Hereafter referred to as CEC.

1952). An understanding of how and why plant species differ in their capacities to adsorb nutrient ions from a given growth medium may lead to a better understanding of ion adsorption by plants.

The purpose of this study was to examine the differences in CEC of various plant roots in order to extend the knowledge of iron adsorption and absorption by plants. The answers to the following specific questions were sought:

1. Is the CEC of plant roots a constant?
2. Is the section or region of a root showing the greatest uptake of a cation such as iron related with the region of the highest CEC?

SECTION I

INFLUENCE OF AGE ON CEC OF PLANT ROOTS

Introduction and review of literature

A considerable amount of work has been done on the determination of root CEC (Drake et al. 1951, Graham and Baker, 1951, and McLean et al. 1956). From CEC values reported by these workers and others, it is concluded that the CEC of monocotyledonous plant roots is generally lower than that of dicotyledonous plants.

Even though these generalities are made, a study of the CEC values reported in the literature shows considerable variation between workers for a given plant species. Some of this variation may be explained by such factors as differences in the methods used in determining the CEC, differences in nutritional status (Wander and Sites, 1956, McLean et al. 1957, and Huffaker and Wallace, 1959), and environmental conditions such as temperature (Williams and Coleman, 1950).

Also, it may be due to differences in the root samples used in determining CEC. Drake et al. (1951) used complete root systems whereas Smith (1955) and Bell (1957) used small sections obtained near the root tip.

The ages of the plants used by the various workers differed. This would undoubtedly cause variation in the CEC values obtained. Although no work to determine this effect has been carried out, there is some indication that the root CEC might change with age (Smith, 1955, and Bell, 1957).

It was felt that this aspect of variance in CEC would be worthy of more critical study. In addition some measure of the variation

introduced by changes in the location of the apportioned amount of root sampled for CEC determinations should be obtained.

Experimental methods

Various methods are used for determining root CEC. In most cases the root is first saturated with a cation, then immersed in a replacing solution and the replaced ion determined analytically. Williams and Coleman (1950) saturated the roots with Ba^{++} or NH_4^+ ions. The amounts of these ions removed by the replacing solution were determined chemically. Some workers saturated the roots with H^+ ions either by immersion in CO_2-saturated water or by electrodialysis (Drake et al. 1950, Smith, 1955, and Bell, 1957). The H^+ ion removed by the replacing solution was titrated with a base to the original pH of the replacing solution. Huffaker and Wallace (1959) used a method whereby they saturated the roots with a radioisotope of zinc and determined the amount of adsorbed zinc using a scaling unit. The CEC values obtained by Huffaker and Wallace (1959) using the zinc radioisotope method are lower than those of other workers (Smith, 1955, and Bell, 1957) using the electrodialysis method.

In order not to handle radioisotopes more than necessary and since more information in the past was obtained using the electrodialysis-titrating method, the latter was chosen as the one to be used in this study.

The CEC of a large number of plant species has been determined, and included in these are varieties which are resistant or susceptible to chlorosis. Corn and barley were chosen to represent the resistant species and beans the susceptible species. A factor aiding in the selection was that the majority of the CEC work reported in the literature is on these plants.

The varieties used in this study were Kingscrost (KY7) corn (Zea mays), Atlas barley (Hordeum vulgare) and Great Northern beans (Phaseolus vulgaris). All seeds were treated using a mercurous fungicide to deter molds during germination.

The corn was germinated by placing the seeds on a perforated porcelain plate in a large glass vessel in which distilled water was brought up so that it just touched the seeds. To aid germination 1 ml. of saturated $CaSO_4$ solution was added to each gallon of distilled water. After germination the level of the distilled water was raised so that the developing roots would not dry out. Aeration of the solution was started at this time. Corn plants were large enough to transplant 5 days after setting the seeds to germinate.

Barley was germinated under conditions similar to that of the corn, and plants large enough to transplant were obtained 5 days after starting germination.

Beans were germinated in sterile, coarse, quartz sand since the root system developed by beans did not lend itself to using the perforated porcelain plate. The perforated porcelain plate is preferred to any other method because it developed roots free from any foreign material, and no damage occurred to the roots when the plants were transferred to the nutrient solution jars. The $CaSO_4$-distilled water was used in germinating beans also. When the beans were 5 cm. high they were ready to be transplanted. This was usually at 9 days after setting the seeds to germinate.

All the seeds set to germinate and the resulting plants were selected for uniformity in size, shape and color.

After germination, when the plants were about 5 cm. high, they

were set out in 1-gallon jars containing full strength Hoagland's #2 nutrient solution (Hoagland and Arnon, 1950). Iron was supplied in a chelated form at 5 ppm. (Giegy Sequestrene 330-Fe).

A yellowing of the corn leaves developed when the iron in the nutrient solution dropped below 1 ppm. This disappeared upon daily addition of chelated iron solution. The pH of the nutrient solution was maintained between 5.5 and 6.0 by addition of 0.5 N NaOH or 0.5 N HCl when required.

At the onset of the experiment the nutrient solution in the 1-gallon glass jars was changed every 4 days. However, as the plants grew larger the nutrient solution was changed every 3 days in order that the nutrient element balance and the pH could be maintained at the desired range. The interval between changes was shortened to 2 days when the plants were 3 weeks old. Between changes the level of the nutrient solution was maintained at the desired height by adding water. Deionized-distilled water was used in preparing nutrient solutions throughout the experiment.

All the plants were grown in a controlled environment growth chamber which had the following growing conditions:

	Day	Night
Temperature	85± 2° F.	65± 1° F.
Humidity	40± 5%	97± 3%
Day length	14 hrs.	
Light intensity	2,000 foot candles at a height of 1 foot	

A randomized block design with 4 replications was used. Three plants per jar were considered as a sample. The treatments consisted of 20 dates of sampling. The plants were sampled every day for 12 days

after which they were sampled every 3 days for 12 days and the remaining 4 samples were a week apart. If possible the plants were sampled in the morning.

The plants were grown to the age required, then removed from the nutrient solution and placed in a large pan of distilled water in order to facilitate obtaining the desired root sections. Only roots that were healthy, white in color, of equal size, and same type (that is without lateral roots) were taken. The root sections consisting of successive 5 cm. lengths were cut after the tip cm. was excised and discarded. Figure 1 shows the location of the various 5 cm. sections of root obtained. Five cm. root sections taken from the same portion of the root were bunched and loosely tied. Ten to 15 root segments were included in each bundle. These bundles of 5 cm. root sections were rinsed in distilled water and placed in a Bradfield-type electrodialysis cell.

The voltage of the dialysis cell was maintained at 120 volts and the current from 50 to 100 milliamperes. During dialysis an increase in ions in the end cells of the dialysis cell was accompanied by an increase in conductance or inversely by a decrease in resistance. From the basic relationship of resistance to current, a decrease in resistance gives an increased amperage. Any increase in amperage, however, was accompanied by an increase in cell temperature. Since it is not known what the effect of dialysis cell temperature has on the CEC of the root sections, care was taken to maintain the current below 100 milliamperes so that the temperature could be kept low and nearly constant. This was accomplished by flushing the end cells whenever the current reached 100 milliamperes. By keeping the current below

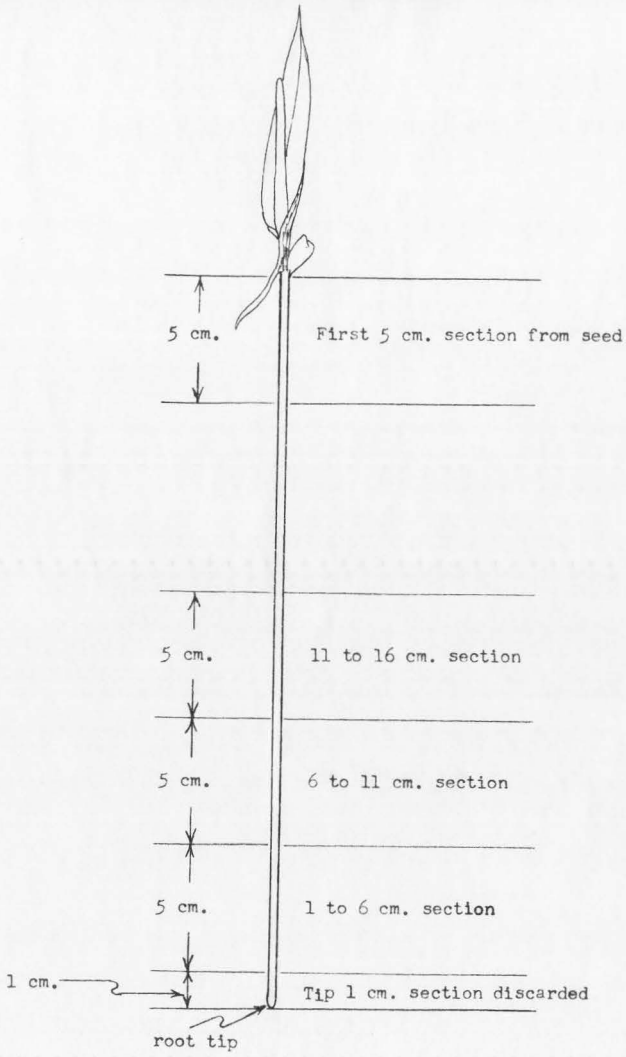

Figure 1. Diagram showing location of root sections used in this study

100 milliamperes and by running water through cooling coils in the dialysis cell, the temperature was kept between 20 to 30° C.

Initial dialysis was hastened by adding a few drops of dilute HCl to the center cell.

After the root sections had dialyzed for 90 minutes they were removed from the dialysis cell, blotted on filter paper for 30 seconds, and then placed in a beaker containing 50 ml. of 1.0 N KCl. This root-KCl solution was titrated using 0.01 N KOH to pH 7 for 5-minute intervals over a period of 15 minutes. Over the titrating intervals the pH of the root-KCl solution was followed using a Beckman Model H pH meter. A microburette capable of delivering quantities down to 1/100 of a ml. was used to add the KOH required to maintain the root-KCl solution at pH 7. The milliequivalents (me.) of KOH used in titrating the root-KCl solution was considered to be equivalent to the root CEC expressed as me./100 g. of dried root material[a].

In the preparation of the 1.0 N KCl solution the pH was adjusted to pH 7 using 0.01 N KOH or 0.01 HCl as required. This pH was checked every day over a period of 1 week in order to achieve a constant pH. At the time of titration the pH of the 1.0 N KCl solution was again checked to see if it was still at pH 7, and if it changed slightly during that period it was adjusted. The pH of the 1.0 N KCl solution is a very critical factor for a small change in the solution left unadjusted would add to or subtract from the ultimate CEC of the roots being titrated.

Results and discussion

Typical changes in me. of KOH used in the 5-minute titrating

[a] Henceforth referred to as me./100 g.

intervals are shown in Figure 2. The number of me. of KOH used to titrate the root-KCl solution in each 5-minute interval was always greater than the number of me. of KOH used in the subsequent 5-minute interval. This phenomenon is not peculiar to this study, but has been found by Smith (1955) and Bell (1957); nor is it common only to the H^+ ion, for it has been found with other ions (Coleman and Williams, 1950). It can be speculated that this phenomenon occurs as a result of the large amount of H^+ ions occupying sites at or near the surface of the root that are immediately available for exchange. Other H^+ ions would be slowly available as the sites they occupy are more to the interior of the root and greater lengths of time would be required for the K^+ exchanging ions to get to them.

When the roots were added to the 1.0 N KCl solution a large change in pH occurred. This change of 2 to 4 pH units changed the pH of the original 1.0 N KCl solution from pH 7 to pH 5 or pH 3. The size of the pH change depended on the type of plant, section of the root, and the number of segments used. Bean root segments always caused a larger drop than did the same segments of corn or barley roots.

All the titrations were carried out using a microburette in which 1 drop was equal to 1/100 of a ml. A small over-titration of a drop or 2 did not appear to affect the CEC obtained for that root sample. Although the titrations were obtained at 5-minute intervals over a period of 15 minutes, only the values for the first 5-minute interval were used in the study. This procedure was followed in order that a comparison with the results of other workers could be made as many of them used only a single 5-minute titrating interval.

Changes in the CEC of various 5 cm. sections of corn roots with

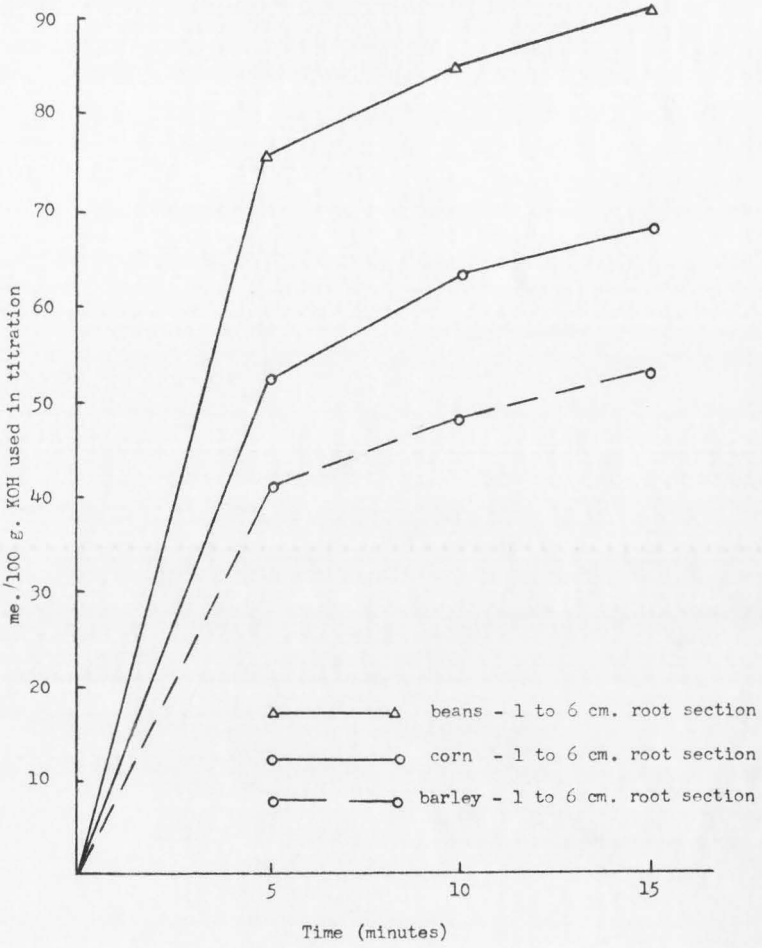

Figure 2. The me. of KOH added to dialyzed root-KCl solution during 5-minute titrating intervals.

age are shown in Figure 3. The CEC of the 1 to 6 cm. root section started near 50 me./100 g. at an age of 5 days. At the age of 10 to 12 days the CEC of this root section rose to a high of 91 me./100 g. and then dropped to 30 me./100 g. at the 15-day age. The CEC of this corn root section remained at this level.

Roots sampled at the 4-week age showed a rise to 50 me./100 g. in the CEC value of the 1 to 6 cm. corn root section. However, what undoubtedly happened is that root segments of younger lateral roots were included in the sample. This could have occurred due to the following reason. Lateral roots that developed looked in all appearances like the older roots that were supposed to be sampled. Shorter lateral roots that developed near the tips of the larger corn roots had a CEC of 88 me./100 g. for the 1 to 6 cm. section. Taking this value for lateral roots and adding to it the CEC value for the 1 to 6 cm. section of the older roots, a figure of 118 is obtained. Dividing this by 2 a figure of 59 is obtained. This value is very close to that shown for the 1 to 6 cm. section of corn roots at 4 weeks. Since the value beyond 4 weeks is unreliable, the value of 30 me./100 g. will be considered as the final value for the 1 to 6 cm. section of corn roots.

At the end of 10 weeks the corn roots were so tightly packed into the 1-gallon jars that the roots developed first could not be distinguished from those that developed later. The CEC of the 1 to 6 cm. sample from all roots at this time was 38 me./100 g.

Changes in the CEC of the 6 to 11 cm. section of corn roots with age followed a pattern similar to that of the 1 to 6 cm. section. As in the 1 to 6 cm. root section, the CEC of the 6 to 11 cm. section started off with a low value of 22 me./100 g. at an age of 5 days,

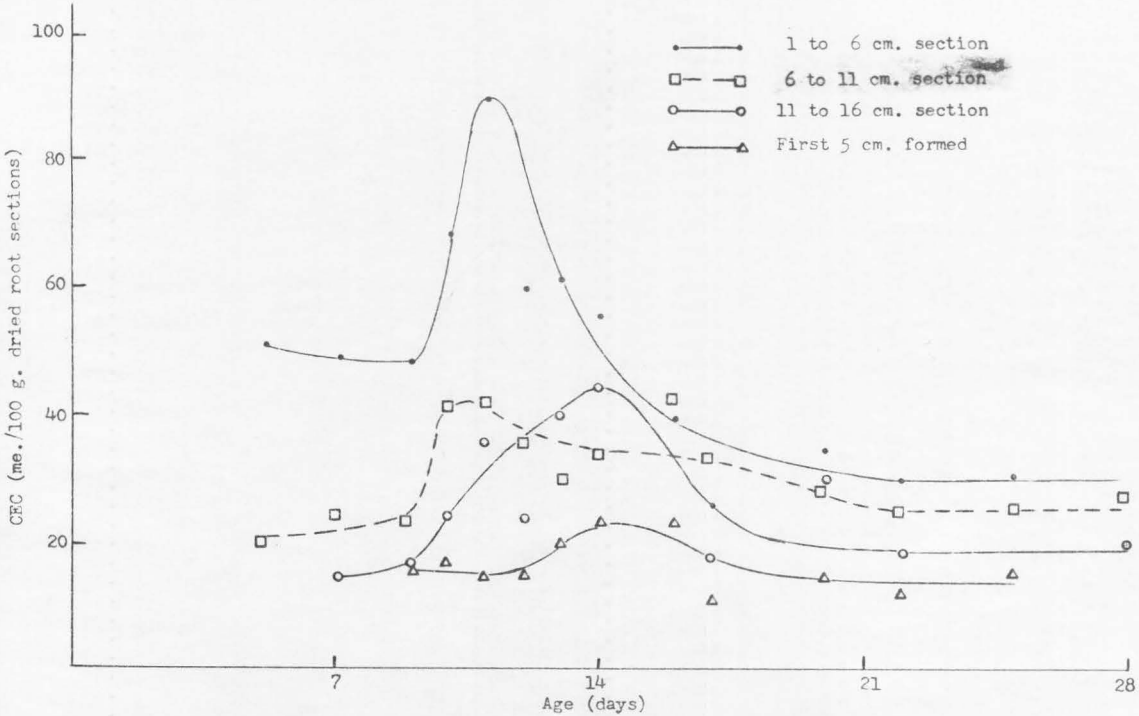

Figure 3. Changes in CEC of various corn root sections with age

rose to a peak of 43 me./100 g. at the 10 to 12 day interval, and then dropped to 23 me./100 g. The data after 5 weeks indicated a rise in the values of CEC obtained. These were not plotted for the same reason that was given for disregarding the rise in the 1 to 6 cm. root section's CEC. The final CEC value of the 6 to 11 cm. section of corn roots will be considered as 23 me./100 g.

The 11 to 16 cm. section of corn roots started with a CEC lower (15 me./100 g.) than that of the previous 2 sections, but developed a CEC higher than that of the 6 to 11 cm. section of corn roots at approximately 2 weeks after germination. The CEC of the 11 to 16 cm. section of corn roots could not be obtained at 5 days as it had not formed yet. Therefore, the first determination of CEC on this root section was at 1 week. At an age of 1 week the CEC of the 11 to 16 cm. section was 15 me./100 g. At the 2-week age the 11 to 16 cm. section had a CEC of 46 me./100 g., after which the CEC dropped off slowly to a low value at 23 days of 20 me./100 g. A rise in CEC of this section after 5 weeks can be disregarded for the reason given for the 1 to 6 cm. root section.

The next 5 cm. section of corn roots studied was that part first formed nearest the seed. This section's CEC was studied only after the root was long enough to produce the other 3 sections required. At a plant age of 9 days the CEC of the first formed 5 cm. was 16 me./100 g. There was a slow rise of the CEC to 24 me./100 g. at an age of 15 days after which it gradually fell to 13 me./100 g. at 22 days.

Changes in the CEC of barley roots with age are shown in Figure 4. The 1 to 6 cm. section at 5 days had a CEC of 52 me./100 g. This sec-

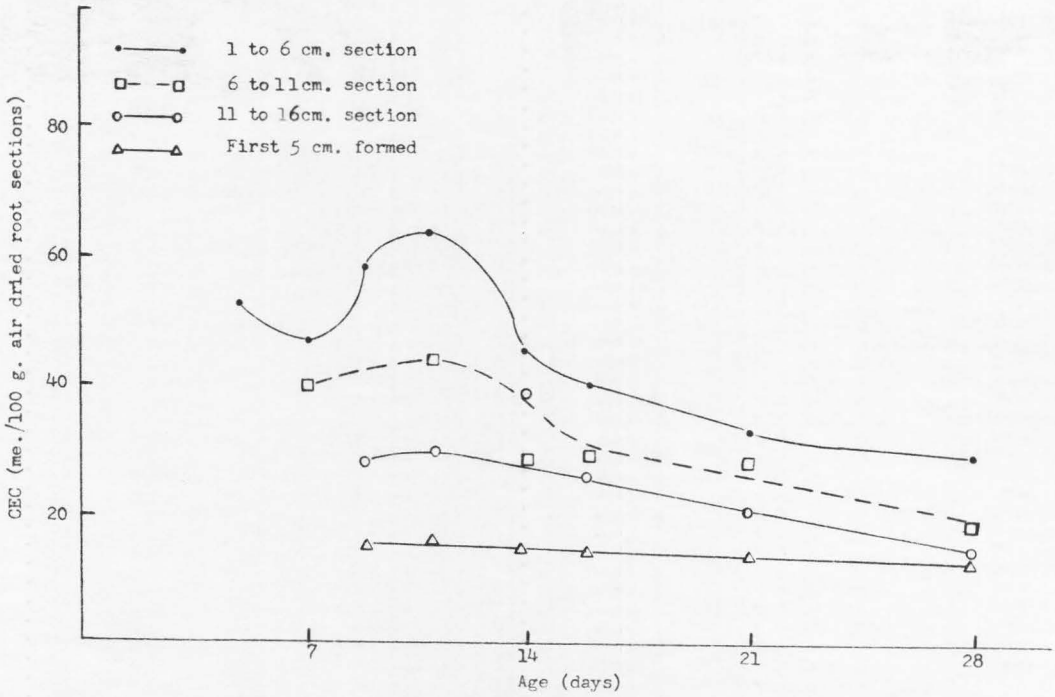

Figure 4. Changes in CEC of various barley root sections with age.

tion's CEC rose slowly to a peak (64 me./100 g.) after which it gradually fell to a value of 29 me./100 g. As in corn, the 6 to 11 cm. section started out lower than that of the 1 to 6 cm., proceeded to rise to a peak at 10 days and then slowly dropped off to a value of 19 me./100 g. A much lower starting value than that of the 1 to 6 cm. or 6 to 11 cm. sections was obtained (28 me./100 g.), which with age rose very little and then gradually dropped off to a value of 16 me./100 g. The first 5 cm. of root formed started with a CEC of 15 me./100 g., rose 2 me. and then dropped off to a value of 14 me./100 g.

The variations with age in the CEC of beans are shown in Figure 5. All the sections followed a pattern quite different from that of corn or barley in that they started out lower than either of these and rose gradually to a value of 88 me./100 g. at 6 weeks without reaching the peak at 10 to 12 days.

A 3-week comparison of the CEC of corn, bean and barley root sections is shown in Figure 6. Only the 1 to 6 cm. root sections were compared in this figure. This was done to examine the CEC of the root section that is considered by many workers to be the most important segment in the uptake of nutrients.

As pointed out previously in the discussion, the CEC of the 1 to 6 cm. section of corn roots started at 50 me./100 g. at the 5-day age, rose sharply to a high of 91 me./100 g. at the 10 to 12 day age, and then it dropped off to a value of 30 me./100 g. At 5 days the 1 to 6 cm. barley root section had a CEC of 52 me./100 g. Quite similarly to that of corn roots, the CEC of the 1 to 6 cm. section of barley roots rose to a peak (64 me/100 g.) after which it fell and leveled off at 3 weeks (29 me./100 g.). Barley root sections appeared to have

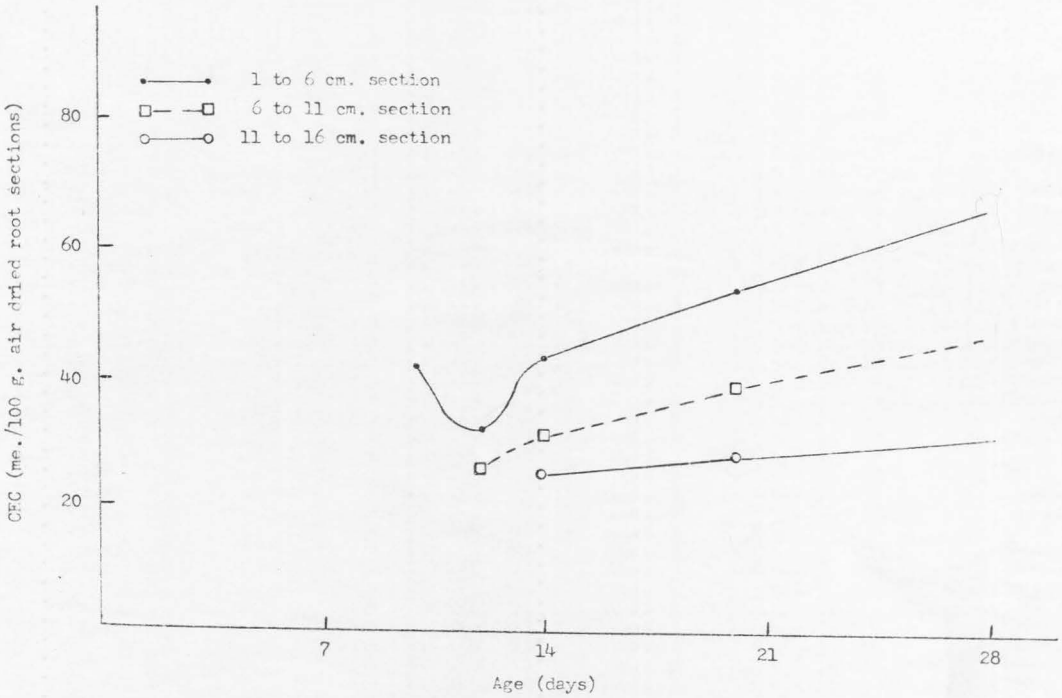

Figure 5. Changes in CEC of various bean root sections with age.

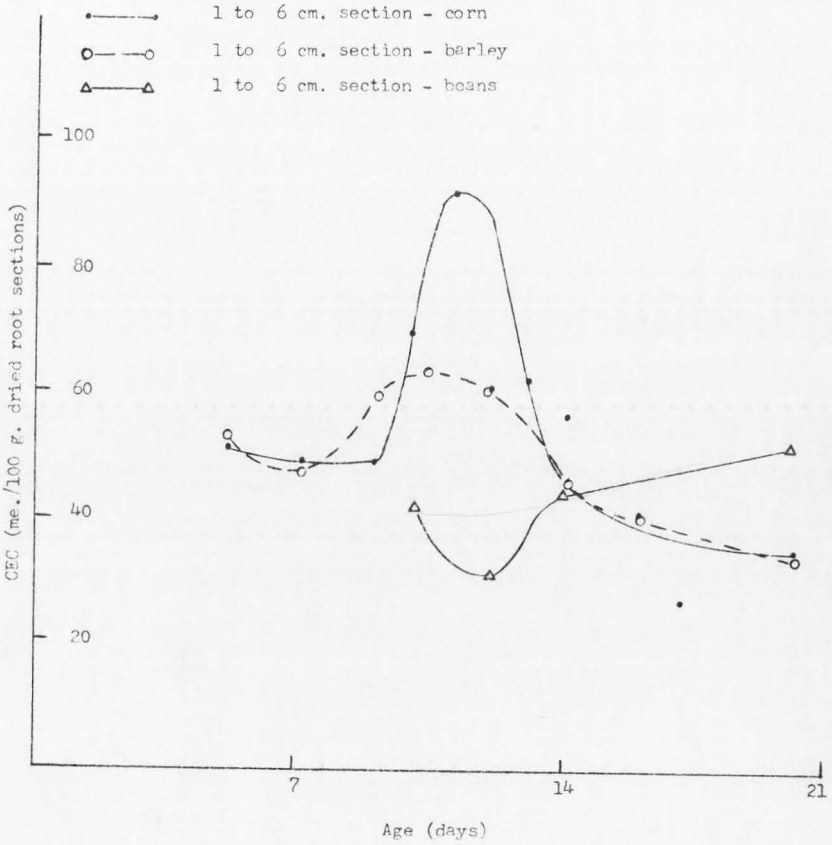

Figure 6. Changes in CEC of corn, barley, and bean root sections with age.

a more gradual rise and fall in CEC around the peak than did corn roots. The CEC peak in barley root sections, however, appeared at the same age as it did in corn roots.

A lower starting CEC was measured on the bean roots than on barley or corn roots (42 me./100 g.). A CEC peak did not show itself in the bean roots as it did in barley and corn. Rather a drop in the CEC of bean roots occurred after which it slowly rose day by day until it surpassed that of barley and corn at approximately 15 days. At 10 weeks the bean roots had a CEC of 88 me./100 g.

A drop occurred in the CEC curve for corn, barley and beans just after the plants were placed in the nutrient solution. This could be due to a certain amount of setback as a result of some slight damage they may have received in the transplanting operation. The corn and barley did not have as large a drop as did beans. This could be expected since the corn and barley were grown on a perforated plate and little or no disturbance of the roots occurred when they were moved to the 1-gallon jars. Beans on the other hand were grown in coarse sand and even though great care was exerted in removing the plants from their germinating media to the 1-gallon jars, a certain amount of root damage resulted. This slight increase in the amount of damage to the beans may be the reason for the larger drop in the CEC after transplanting.

It is indicated by the data presented in Figure 6 that in order to compare plant mineral composition on a CEC basis, care must be taken to insure that all plants are of equal age. At an early age corn and barley had a higher CEC than did beans. At later ages, however, there was a reversal of plant CEC. If the mineral composition of corn plants 2 weeks old or younger were compared to bean plants of equal age, it

would be difficult to explain species composition differences on the basis of measured root CEC. On the other hand in comparing the mineral composition of plants 3 weeks old or older, no difficulty should be encountered using the above procedure.

At this point a comparison of the data obtained in this study with that in the literature might be in order. A summary of the root CEC of a number of plant species, as given by a number of workers, is presented in Table 1. This shows that the CEC of dicotyledonous plants is higher than that of monocotyledonous plants.

The values reported in Table 1 differ from worker to worker. This is not too unusual as they used different varieties, plants of different ages, different root samples, different methods of saturating the roots with hydrogen or other cations, varied methods and times of titration, and replacement of adsorbed ions. Therefore, the relative CEC values for plant species given by various workers should be considered rather than the absolute values of the root CEC.

A comparison of the CEC values of barley, bean and corn roots found in this study and that for the same plants as reported by other workers is presented in Table 2. A first glance at the table appears to give an indication of a marked discrepancy between the CEC values found in this study and those reported in the literature. This, however, is not the case. The CEC values of corn roots presented by Bell (1957) are at an age of 9 and 14 days. This agrees well with the present study, for the 9-day values would be on the rising part of the CEC peak or on the falling side depending on when the age of corn was determined by Bell (1957). If the age of corn was determined from the beginning of germination the 9-day CEC values would be on the rising

Table 1. Values of cation exchange capacity of various plants reported by various workers

Plant	McLean and Baker (1953)	Drake et al. (1951)	Graham and Baker (1951)	Smith (1955)	Bell (1957)	McLean et al. (1956)
			me./100 g.			
Great Northern bean				53		
Milo	17					18
PI soybean	41	59	43			54
Pea		50				
Rye		15	26			
Wheat		9	22			
Barley		12	24-26	23		13
Corn		22		26	46-23	11
Tomato		35				
Oats			24			19-23
Alfalfa	42					46
Red top	14					17
Reed canary	12					14
Cotton						40
Vetch						54
Rice						15

Table 2. Cation exchange capacity of excised roots from a number of plants as reported by various workers

Worker		Plant species					
		Corn		Barley		Beans	
		CEC	Age	CEC	Age	CEC	Age
		me./100 g.	Days	me./100 g.	Days	me./100 g.	Days
Bell	(1957)	46-23	9-14				
McLean et al.	(1956)	25	15	13	14		
Drake et al.	(1951)	22	10	12	10		
Smith	(1955)			23	21-42	53	10
Graham and Baker	(1951)			24 27	56 35		
Present study	(1959)	91-26	10-21	64-29	10-21	30-88	10-42
Kamilia		3-20				12-68	

side of the peak. Five to 6 days after germination are required to obtain plants of sufficient size to place into nutrient solution. Had the age of the corn plants been decided as 9 days after setting the plants into nutrient solution, they would have been 14 or 15 days old and consequently the reported CEC would be on the declining side of the curve. In either case the smaller value of 23 me./100 g. given at 14 days agrees with the lower value of corn in the present study at the same age. Drake et al. (1951) probably started to count the age of corn plants from the time of setting plants into nutrient solution and, as such, the reported value of 22 me./100 g. at 10 days would be closer to 15 or 16 days and would agree with the data in the present study. The values obtained by McLean et al. (1956) compare with the values obtained in this study and with those reported by Bell (1957) and Drake et al. (1951). The values given by Graham and Baker (1951) and Smith (1955) agree with the values obtained for barley at the 3 to 8 week age. The 64 me./100 g. listed from the present study is the peak value for barley in Figure 6, but the CEC of the barley roots continued to fall and at the end of 4 weeks had a value of 29 me./100 g. The latter CEC value agrees with those reported.

The value given for beans at the 12-day age by Smith (1955) is 12 days after placing into solution and not 12 days after first starting to germinate. In this study the ages are given for days after beginning of germination, thus the ages for the beans reported by Smith (1955) would be approximately 1 week older and the values would agree with those in this study at the end of 20 days (Figure 6). The CEC of bean roots in this study started at 30 me./100 g. and continued to rise until at 6 weeks it attained a value of 88 me./100 g.

Care should be taken in interpreting the values obtained for the root CEC. The roots sampled would not always be of the same metabolic age, which may be the reason for the scattering of points in Figures 1 and 2.

The changes with age in the heights of aerial portions and the lengths of roots of plants used in this study are presented in Table 3. This table is included not as a means for critical comparison, but to show the relative changes with age of the root and aerial portions of these plants.

Summary

Changes in the CEC of excised root sections were studied. Sections of plant roots were electrodialyzed in order to saturate all exchange sites with hydrogen ions. Immersion in a salt solution replaced the exchangeable hydrogen which was subsequently titrated. The milliequivalents of base used to titrate the hydrogen for a 5-minute interval was considered to be equivalent to the root CEC.

Corn and barley root CEC started off low, rose to a peak at 10 to 12 days and then fell to a level below that at which it started. The CEC of root sections excised from plants 3 weeks old or older remained low.

Bean root CEC on the other hand started off lower than that of corn and barley, but proceeded to slowly rise until at approximately 3 weeks it surpassed that of corn and barley and continued to rise until it reached a level of 88 me./100 g. at a 5-week age.

The 1 to 6 cm. root sections had the highest CEC of all sections studied in all plants used.

Table 3. The changes with age in the heights of aerial portions and the lengths of roots of plants used in this study

Plant	Portion Measured	Age (days) 5	6	8	10	12	15	35	70
					length (cm.)				
Corn	Roots	10-15	15-20	25-30	35-45	45-55	50-60	65-80	100
	Aerial	11	15	24	31	37	45	75	125+ tasseling
Barley	Roots	5-7	8-10	10-12	15-20	22-27	30-40	45-55	
	Aerial	7	8	10	12	16	18	40	
Beans	Roots				10-20	20-30	35-45	50-60	
	Aerial				10	14	20	45 flowering	

SECTION II

CATION EXCHANGE CAPACITY OF SMALL ROOT SEGMENTS

Introduction

In order to obtain a more detailed picture of the change in CEC of plant roots, portions of the root smaller than 5 cm. in length should be studied. From the literature (Bell, 1957) and from consultation with members of the Agronomy and Botany departments at Utah State University, it was decided that 1 cm. sections of the roots would be the most feasible units to study. It was also decided to use the 1 cm. sections of the root containing the root tip. This section was discarded by previous workers prior to making CEC measurements for it was felt that the increased meristematic activity of the growing root tip might have some effect on the CEC measurement.

Experimental methods

The equipment used in the previous portion of the study could not be used for the 1 cm. root sections, so dialysis cells which would handle the smaller root sections were designed and built (Figure 7). Five dialysis cells were constructed so that the first five 1-cm. sections of plant roots could be studied at one time. These cells were made from plexiglass tubing with an outside diameter of 5/8 inch and an inside diameter of 1/4 inch. To insure better dialysis the diameter of the end cells was widened to accommodate an electrode as large as the inside diameter of the center cell. The larger dialysis cells used in Section I had cooling coils which enabled the maintenance of a low cell temperature despite increases in amperage. However, the smaller cells were too small to provide space for cooling coils. Therefore,

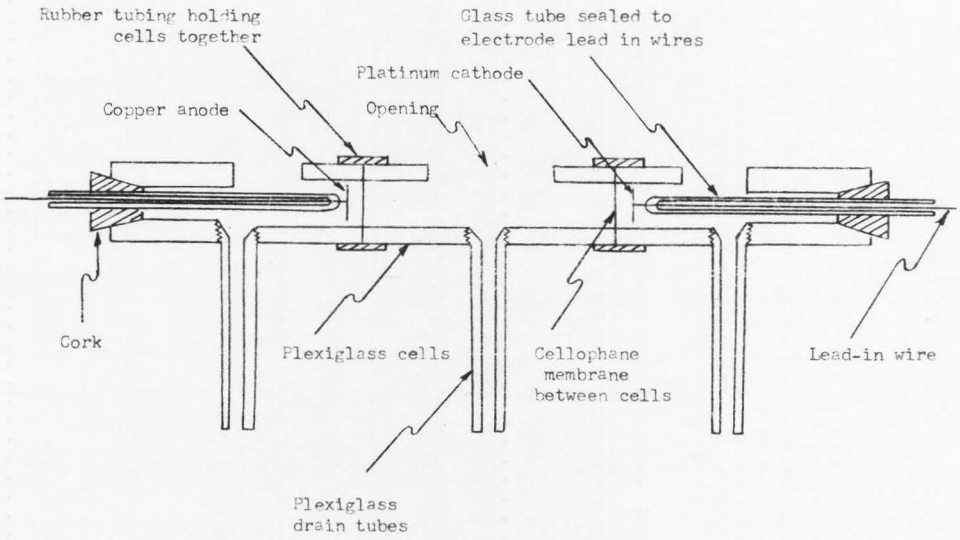

Figure 7. Diagram of electrodialysis cells used for experiments with 1 cm. root sections (actual size).

the only alternative left for controlling temperature was through fine control of the dialyzing current accomplished by frequent flushing of the end cells throughout the time of dialysis. In order to provide a swifter means of reading the current in the dialysis cells than was used in Section I, a switch was constructed which enabled reading the amperage and voltage in one cell without disrupting the dialyzing current in the other 4 cells. This switching mechanism employed a multicontact dial switch with separate leads to all the cells in any reading position. Incorporated with the dial switch was a multicontact push button switch which enabled reading either voltage or current in the cell without disrupting the dialyzing process. The temperature was kept between 20 and 45° C.

The same varieties of plants with the exception of barley were used in this study: Kingscrost (KY7) corn (Zea mays), Great Northern beans (Phaseolus vulgaris), and, in addition, 2 varieties of soybeans were included. They were PI 54619-5-1 soybeans and Hawkeye soybeans (Glycine max). There were included to enable comparing a variety which is resistant (Hawkeye) with one that is susceptible (PI) to lime-induced chlorosis.

As in Section I, a randomized block design with 4 replicates was employed. Sampling dates were considered the treatments. Three dates of sampling were used so that a comparison could be made in ages before and after the 15-day period when crossing of the CEC values of dicotyledonous plants and monocotyledonous plants occurred. Sampling dates were 10 to 14 days, 3 weeks and 5 weeks.

Plants were grown in full strength Hoagland's #2 nutrient solution (Hoagland and Arnon, 1950) as given in the previous section. At

the desired age plants were removed from the nutrient solution, the roots rinsed in distilled water, and then the first 5 cm. from the root tips were cut into 1 cm. sections and placed in the small dialysis cells. Ten to 15 segments were included in each sample. The location of the excised root sections in relation to the entire plant is shown in Figure 8. The excised root sections were dialyzed for 90 minutes at 120 volts and at a current ranging from 50 to 100 milliamperes. After dialysis the root sections were removed, blotted for 30 seconds on filter papers, and placed in a beaker containing 100 m. of 1 N KCl solution at pH 7. The root-KCl system was kept at pH 7 by titrating with 0.01 N KOH for 5-minute intervals over a period of 15 minutes. The me. of KOH used to titrate the root-KCl system for the first 5-minute interval was considered to be equivalent to the CEC of the particular root sections, expressed as me./100 g. of dried root material.

A magnetic stirrer was used to mix the root-KCl system during the titration.

Results and discussion

The magnetic stirrer used to mix the root-KCl system during the titration had the tendency to crush or shred the 1 cm. root sections. This crushing tendency was especially manifest on the 1 cm. sections of younger roots of dicotyledonous plants. For this reason the CEC of 1 cm. root section of beans at 10 to 12 days, and of soybeans at 10 to 12 days and 3-week ages was not obtained.

The CEC of the 1 cm. sections of various plant roots studied in this section is shown in Table 4. The average CEC is presented so that a comparison can be made with the 1 to 6 cm. root sections used in

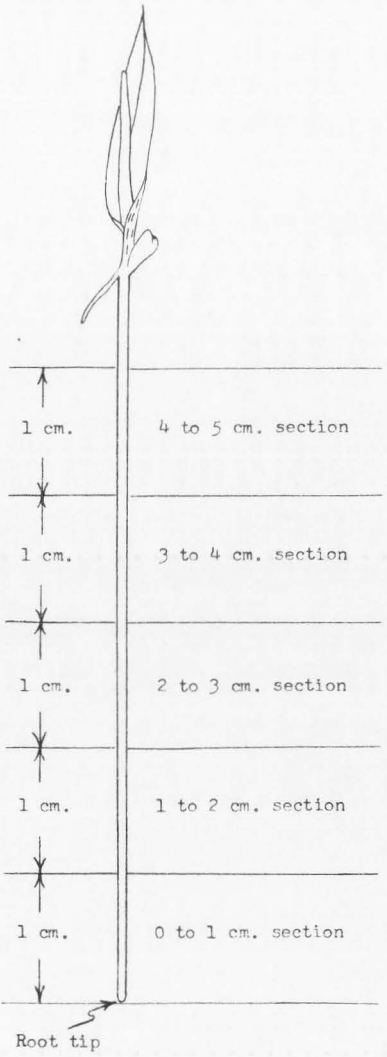

Figure 8. Diagram showing the location of the excised root segments used in Sections II and III.

Table 4. CEC of plant roots as related to age of plant and section of root sampled

Root Section	Plant species and age of plant						
	KY7 corn			Great Northern beans		Soybeans	
						Hawk-eye	PI
	10-12 days	3 wks.	5 wks.	3 wks.	5 wks.	5 wks.	5 wks.
	me./100 g.						
0 to 1 cm.	45	65	46	47	122	88	110
1 to 2 cm.	233	113	103	123	138	139	164
2 to 3 cm.	139	87	54	89	79	131	109
3 to 4 cm.	74	78	61	63	85	110	89
4 to 5 cm.	32	37	35	38	64	59	92
Average	105	76	60	74	98	105	111

Section I. In all cases the average CEC of the 1 cm. root sections for a species at a given age is higher than the corresponding 1 to 6 cm. section for the same plant and age in the previous section. This may be due to several factors. The 0 to 1 cm. root section was excluded from the 5 cm. root lengths used in Section I, and since the 0 to 1 cm. length has a higher CEC than the 5 to 6 cm. it would tend to raise the average CEC. Difficulty encountered in stirring the root-KCl system caused some crushing of the roots. Any loss of root material included in the 1 cm. root samples would have made a larger CEC than a similar loss with 5 cm. lengths where a larger total root weight was used. There could also be a quicker and better replacement of K^+ for H^+ in the 1 cm. root sections which could give a higher CEC as well. Bell (1957) showed that the cut ends of the root segments had no effect on the CEC values obtained for corn. Since the number of root segments used in this study is far greater than that used by Bell, the effect of cut ends may be of some importance. An increase in cut ends may have given an increased CEC by making the interior of the root more accessible for replacement or exchange of ions.

At the 3-week age the CEC of the 0 to 1, 3 to 4 and 4 to 5 cm. sections of corn roots was higher than at the 10 to 12 days or 5 weeks. This change with age is different from that of the 5 cm. root sections given in Section I. The CEC of the 1 to 2 and the 2 to 3 cm. segments is the same as that given in the previous portion of the study, in that it decreases with age from a high at 10 to 12 days to a low at 5 weeks. The 1 cm. root segments with low CEC values are the ones with the greatest deviation from the set CEC pattern. While individual segments appeared to differ from the CEC pattern for corn, the overall average

pattern was the same. The largest change was in the 1 to 2 and 2 to 3 cm. segments.

Except for the 2 to 3 cm. segment all the bean root segments followed the pattern set by larger sections in the first part of this study, in that the CEC increased with age. The largest increase was found in the 0 to 1 cm. section. As with corn, the discrepancy of individual 1 cm. sections from the CEC pattern set in Section I was in the segments with lower CEC values. The average values agree with the previously established CEC pattern.

Although discrepancy exists in the CEC values given for soybeans in the literature, the values presented by Drake et al. (1951) and McLean et al. (1956) would lead one to believe that soybeans have a slightly higher CEC than do beans. The average values presented in Table 3 for both PI and Hawkeye soybeans are in line with this expected trend. The individual 1 cm. soybean root sections differed from that of beans and differed between the two soybean varieties studied. Hawkeye soybeans had a much lower CEC for the 0 to 1, 1 to 2 and 4 to 5 cm. sections than did PI soybeans. The other two sections of Hawkeye soybeans (2 to 3 and 3 to 4 cm.) had CEC values higher than those obtained for the PI variety. The 1 to 2 cm. section of the PI variety showed much larger CEC than the same root section of the Hawkeye soybeans.

Summary

Root sections 1 cm. long were studied in order to obtain a more detailed picture of the change in CEC with age. These root sections were electrodialyzed in order to fill all exchange sites with hydrogen ions. The hydrogen ions on the exchange sites were removed by immersion

in a salt solution and subsequently titrated. The quantity of base used in the titration was considered to be equivalent to the CEC expressed as me./100 g. dried root material.

The CEC values of 1 cm. segments of corn, beans and PI and Hawkeye soybeans were obtained. Average values of the 1 cm. segments, although higher, were in agreement with those obtained for the 5 cm. root sections of the same plant at the same age (Section I). CEC changes in the 1 to 2 cm. sections of all roots sampled followed the pattern set by the previously studied 5 cm. sections. For all plants at any age the 1 to 2 cm. sections had the highest CEC of all the sections studied.

The CEC values of the 1 cm. corn root sections decreased with age. The CEC values of the same segments of beans rose with age. Beans and soybeans at the 5-week age had higher CEC values than did corn. From the values obtained here and in Section I, it can be predicted that at the 10 to 12 day age 1 cm. sections of corn roots would have higher CEC values than would bean and possibly soybean root sections.

SECTION III

CATION EXCHANGE CAPACITY OF PLANT ROOTS AND UPTAKE OF IRON

Introduction

It has long been felt that the uptake of nutrient cations by the plant root is first of all an exchange reaction. Overstreet and Jacobson (1952) have shown that an exchange reaction actually takes place in the transfer of nutrient cations from the growth media to the root. This is accomplished by exchange of hydrogen, hydroxyl, or bicarbonate ions on the root surface for nutrient ions of the substrate. As it is considered an exchange reaction, the CEC of the root should have an effect on the amount of cation adsorbed on the root surface and subsequently absorbed by the root.

Smith (1955) and Wiebe (1953) pointed out that the amount of nutrient ions adsorbed and absorbed by plant roots could be determined by using radioisotopes of the nutrient ions of interest. Root sections are immersed in radioactive solutions and withdrawn after a certain period of time, placed in a replacement solution and then removed following a prescribed length of time. The amount of radioisotope removed by the replacing solution is considered that adsorbed while the amount remaining on or in the roots is considered that absorbed.[a]

Experimental methods

Radioisotope Fe^{59} was used as an aid in determining adsorption and sorption of iron by the root. A solution of $FeCl_3$ having an Fe concentration of 1,000 ppm. was made and to it was added an aliquot

a Henceforth absorbed referred to as sorbed.

of Fe^{59} solution. The specific activity of this solution was then obtained. $FeCl_3$ stock solution (1,000 ppm. iron) had a pH of 4.0.

A preliminary experiment was carried out to decide the length of time that excised root sections should remain in the 1,000 ppm. Fe* solution and the replacing 0.01 N KCL solution. This experiment was a 3 X 5 factorial with 3 replications. Five lengths of time in the Fe* solution were combined with 3 lengths of time in the 0.01 N KCl replacing solution. The most suitable immersion time is that beyond which little or no change occurs in the amount of Fe* adsorbed or sorbed by root sections.

Bunches of 10 to 15 sections of corn root 1 cm. long were placed in the solutions at the various time combinations. The Fe* removed by the salt solution and that which remained on the root were determined in a well counter using a Nuclear 183 scaler.

The amount of Fe* adsorbed and sorbed by the corn root sections under varying times in Fe* and KCl solutions is shown in Table 5. The amount of sorbed Fe* increased as the length of time in the Fe* solution was increased. However, beyond a 2-minute immersion there was very little change in the amount of sorbed Fe*. Therefore, the 2-minute immersion time was chosen. As the length of time in the replacing KCl solution was increased, the amount of adsorbed Fe* increased. Immersion times longer than 1/2 minute in the KCl solution gave very little change in the amount of Fe* adsorbed. Therefore, the 1/2 minute time was chosen. An immersion time of 2 minutes in the Fe* solution followed by a 1/2 minute dip in the 0.05 N KCl solution gave results that parallel very closely those of longer duration.

* Indicates radioisotope Fe^{59} added to label the Fe solution.

Table 5. The amount of Fe* adsorbed and sorbed on excised corn root sections under varying times in Fe* and KCl solutions

Time in 0.05 N KCl solution	Type of Fe* associated with the root	Time in Fe* solution (minutes)				
		1/2	1	2	5	10
(minutes)		cpm/g. dried root material				
1/4	Adsorbed	233	310	315	321	321
	Sorbed	453	696	770	771	1076
1/2	Adsorbed	442	454	465	475	489
	Sorbed	454	648	928	948	977
2	Adsorbed	455	459	476	478	478
	Sorbed	488	792	916	940	976

A randomized block design with 4 replicates was utilized in this study. The treatments consisted of 2 dates of sampling: 10 to 12 days and 4 weeks. Two species were used: Kingscrost (KY7) corn and Great Northern beans.

The corn and beans were grown in full strength Hoagland's #2 nutrient solution (Hoagland and Arnon, 1950). At the age required by the experiment the plants were removed from the nutrient solution, the roots washed in distilled water and cut into 1 cm. sections. The similar 1 cm. root sections were bunched, loosely tied with fine wire, rinsed in distilled water and then blotted on filter paper. Ten to 15 root segments were included in each bunch. The root bundles were then placed in 5 ml. of radioactive iron solution, removed after 2 minutes, rinsed 3 times in distilled water, and placed in 5 ml. 0.05 N KCl solution. After 1/2 minute in the 0.05 N KCl solution the roots were removed, rinsed in distilled water, and placed on a rack to dry. The distilled water rinse that followed the KCl solution dip was added to the KCl solution. The bundles of roots were continually agitated manually during the time immersed in each solution. The amount of Fe* removed by the KCl solution was considered as that adsorbed by the root while the amount remaining with the root was considered that sorbed.

The dried roots and KCl solutions were counted in a well counter using a Nuclear 183 scaler.

Results and discussion

The amount of Fe* adsorbed and sorbed by corn root sections is presented in Table 6. It can be seen that the 1 cm. sections of young corn roots (10 to 12 days) both adsorbed and sorbed more Fe* than the

Table 6. Iron adsorbed and sorbed by root sections of corn at various ages[a]

Root Section	Fe* adsorbed		Fe* sorbed	
	10 to 12 days	4 weeks	10 to 12 days	4 weeks
	cpm/g. dried root material			
0 to 1 cm.	416	50	760	643
1 to 2 cm.	536	53	2590	1381
2 to 3 cm.	433	70	3452	1492
3 to 4 cm.	479	53	3542	1637
4 to 5 cm.	421	56	2597	1386

a See text, page 39, for description of adsorbed and sorbed.

comparable root sections at the 4-week age. The adsorption of Fe* seemed to follow a pattern in young and old plants. The greatest amount was adsorbed by the 1 to 2 cm. or 2 to 3 cm. root sections. This pattern is very similar to that exhibited by the CEC of the 1 cm. root sections. The sorption did not follow a pattern similar to that of adsorption. The Fe* sorbed by the root sections of both young and old plants seemed to be highest in the 3 to 4 cm. sections. No correlation can be seen between the amount of Fe* sorbed and the CEC of the root sections.

The amount of Fe* adsorbed and sorbed by bean root sections is presented in Table 7.

As in corn root sections, no correlation can be seen between the amount of Fe* sorbed and the CEC of bean root sections. There was, however, one trend in the Fe* sorption pattern that appeared to be similar in both corn and beans. The 0 to 1 cm. root section had the smallest amount of sorption of all the root sections studied. In corn the highest amount of sorption was in the 3 to 4 cm. section at both the 10 to 12 day age and the 4 week age. In beans, however, there appeared to be a slight change. In the 12 to 14 day old bean roots the 2 to 3 cm. section had the greatest sorption while in the 5-week old beans the 4 to 5 cm. section had the highest sorption of Fe*.

Beans differed from corn in the effect of age on the changes in amounts of Fe* sorbed by the roots. Although the pattern of sorption was the same in corn and bean roots, the amount of Fe* sorbed did not drop off as much with age in beans as it did in corn.

The adsorption of Fe* by bean root sections varied from that

Table 7. Iron adsorbed and sorbed by root sections of beans at various ages[a]

Root Section	Fe* adsorbed		Fe* sorbed	
	12 to 14 days	5 weeks	12 to 14 days	5 weeks
	cpm/g. dried root material			
0 to 1 cm.	605	532	6400	5728
1 to 2 cm.	268	325	7525	5991
2 to 3 cm.	237	263	7996	6238
3 to 4 cm.	273	283	7315	6553
4 to 5 cm.	241	271	7776	6973

a See text, page 39, for description of adsorbed and sorbed.

shown by corn. The 0 to 1 cm. section of bean roots had the highest adsorption of Fe*, whereas this was true of the 1 to 2 cm. section in corn. Except for the 0 to 1 cm. section, the adsorption of Fe* by bean root sections appeared to follow the pattern of the CEC by sections and age. The 0 to 1 cm. sections had a lower CEC than the 1 to 2 cm. sections, yet the amount of Fe* adsorbed was higher. The reason for this was not apparent. With the exception of the 0 to 1 cm. root section, the increase in CEC of bean roots with age was shown in an increase in the Fe* adsorbed.

Summary

The radioisotope of Fe* was used to study the pattern of adsorption and sorption by excised root sections of beans and corn.

With the exception of the 0 to 1 cm. section of bean roots, the amount of adsorption of Fe* followed the CEC pattern. The root section with the highest CEC had the highest amount of Fe* adsorbed.

Sorption of Fe* was not correlated with root CEC.

Less Fe* was sorbed and adsorbed by corn roots at the 4 week than at the 10 to 12 day age.

More Fe* was adsorbed by bean roots at 5 weeks than at the 10 to 12 day age. The amount of Fe* sorbed at 5 weeks was less than that sorbed at the earlier age.

GENERAL DISCUSSION

Various assumptions exist about the chemical constituents of roots which can exchange ions. Pectin of the plant roots had been suspected as being of importance in the uptake of nutrients. Relationship of other root materials such as amino acids and proteins in the outer plasma membrane or phenolic hydroxyl groups of lignin to ion exchange had also been suspected.

Keller and Deuel (1957) undertook a study to determine whether there is a relationship between CEC and the pectin content of plant roots. The results of their study showed that graminaceous roots (corn and wheat) had less pectin and fewer free carboxyl groups of pectin than did dicotyledonous plants (beans, tobacco and tomatoes). According to their experiments, 70 to 90 percent of the CEC of wheat, corn, bean, tobacco and tomato roots is attributable to the free carboxyl groups of pectic substances in plants. The CEC is directly proportional to the pectin content of roots and inversely proportional to the degree of esterification of root pectin.

Huffaker and Wallace (1959) indicated that the root CEC was decreased approximately one-half when pectates were dissolved from the root. They did not say what portion of the pectate was removed. Their study is another indication that the pectates are the most important single contributor to the CEC of plant roots.

Since Keller and Deuel (1957) worked with older roots their findings serve to substantiate the findings of the present study, as beans

and soybeans were found to have higher CEC values than did corn or barley.

Since root hairs are covered by a pectin coating (Howe, 1921), the root hair zone would be expected to have a higher CEC on the basis of the findings of Keller and Deuel (1957). The lengths of 1/2 to 2 cm. from the root apex of the root is considered the region with the highest amount of root hairs (Wiebe, 1953). Higher CEC values for root segments in the root hair zone were found in this study, although root hair density was not studied. In the 1 to 6 cm. section 2/3 of this root hair region was included along with portions of the root without root hairs. The 1 to 2 cm. section was wholly a region of root hairs, whereas the 0 to 1 cm. section had only half as much, and the other 1 cm. segments perhaps a few root hairs or none at all. In all cases the CEC of root segments that included root hairs was higher than that of segments without them. The 1 to 2 cm. section which was entirely a region of root hairs had a very high CEC and was consistently higher than all other segments studied.

A number of studies (Wander and Sites, 1956, McLean et al. 1956, and Huffaker and Wallace, 1959) point out the effect of variation in nutritional status, particularly nitrogen and phosphorus on the CEC of plant roots. Huffaker and Wallace (1959) note that the factors causing changes in root CEC also influenced the total organic acid content in plants. Keller and Deuel (1957) feel that organic acids do contribute to the CEC of plant roots, but to a lesser extent than does pectin.

Undoubtedly the mineral composition of the nutrient solutions varied from time of mixing to time of changing. Changes in the nitrogen status of the nutrient solution were probably greater than

for any other component of the nutrient solution. From the data presented by McLean et al. (1956) and Huffaker and Wallace (1959), it is possible that the CEC of the plants had some cyclic changes introduced due to cycles in the nutritional status. This may have been responsible for variation in CEC values obtained at particular ages and high or low CEC values obtained when the rest of the values were following an established curve.

Data obtained throughout this study showed that the different plant species studied had entirely different root CEC values. However, as pointed out previously, this may be due to an effect of pectin content variation between plant species. The CEC values changed with age, but the different species had individual CEC.

When the CEC pattern obtained for corn and barley (monocotyledonous plants) is superimposed on that obtained for beans a dicotyledonous plant as shown in Figure 6, it was seen that at an early age the CEC of the monocotyledonous plants was higher than that of the dicotyledonous plant. This difference widened as the curve for the monocotyledons rose sharply. However, the gap between the monocotyledon CEC values and those of the dicotyledon quickly closed as the monocotyledon curve dropped sharply and reached a fairly constant low value. At the same time the CEC of the dicotyledonous plant rose slowly and became larger than that of the monocotyledonous plants at an age of approximately 15 days. This change in CEC values of monocotyledons and dicotyledons makes it necessary to stipulate the ages of the plants when making the generally accepted premise that monocotyledonous plants have a lower root CEC than do dicotyledonous plants.

Age of plant roots had an effect on the CEC values obtained.

CEC values of segments obtained in close proximity to the root tip were constantly higher than for segments further from the tip. This may be due to several reasons. There is an absence of root hairs in the regions further from the root tip. Since the root hairs have a high pectin content, lack of them would cause a lower CEC. Older sections of roots become woodier and suberized and would have less pectin, and consequently a lower CEC.

Wiebe (1953) found that absorption of isotopes occurred along the entire length of barley roots. Although absorption occurred over the entire length, the greatest amount was in the terminal 3 to 4 cm. portion of the root. Absorption was gradually reduced in the older portions of the root. The region of highest absorption presented by Wiebe (1953) and Kramer and Wiebe (1952) coincides with the region of highest CEC obtained for barley roots in the present study. The decreasing absorption in the older portions of the root correlates well with the decrease in CEC found in older portions of barley roots in this study.

Short term adsorption experiments as carried out in the present study should have little complication due to metabolic processes and, as such, should give good correlation of adsorption with root CEC. Root segments with high CEC had high adsorption and sorption of Fe*. Although the adsorption and sorption times in the present study were of much shorter duration than those used by Wiebe (1953), the results in both studies parallel each other.

An exception in the present study of correlation of adsorption of Fe* with root CEC was found in the adsorption by the tip cm. segment of bean roots. This segment, although it did not possess the highest CEC, had the highest adsorption of Fe*. A similar peak in

absorption was found for isotopes by Wiebe (1953). The reason for this was not apparent.

In the present study results of adsorption and sorption of Fe* by plant roots correlated well with root CEC.

Since the pH was not known during dialysis or during the time the root segments were immersed in the 1,000 ppm. Fe* solution, the effect of the pH could not be taken into account.

SUMMARY AND CONCLUSIONS

The CEC of excised roots of corn, barley, bean and soybean plants at various ages were studied.

From the data obtained in this study it was concluded that the CEC of plant roots changed with age. This conclusion is based on a number of separate findings. First, the CEC pattern found for various excised sections of corn roots changed with age. This pattern was obtained with all corn root sections studied. The CEC of all the 5 cm. sections of corn roots at an early age (5 to 7 days) started off low, rose to a peak at an age of 10 to 12 days, after which it fell to a value lower than that at which it had started and remained there. The 1 to 6 cm. section had the highest CEC at all times during the study, with the CEC of each subsequent 5 cm. section cut further from the apex of the root lower than that of the previous one. At selected ages along the CEC pattern established for 5 cm. sections, the CEC values for smaller sections (1 cm.) of corn roots were similar in magnitude to that obtained for the 5 cm. sections. In the smaller segments the 1 to 2 cm. section had the highest CEC values.

Second, when the experiment was repeated using excised sections of barley roots, the CEC pattern developed by corn was repeated in that the CEC of all barley root sections started off low, rose to a peak at 10 to 12 days and dropped to a constant low value smaller than that of the starting values. As in corn the 1 to 6 cm. section of barley roots had the highest CEC value. The subsequent sections obtained further

and further from the apex of the root had decreasing values. The absolute CEC values for barley and corn were not the same; similar sections of barley roots were always lower in CEC than corn. The relative changes in the CEC pattern were similar for barley and corn.

The third point in favor of the conclusion is that excised bean root sections also developed a CEC pattern with age, but one that differed completely from that of corn or barley root sections. Bean root sections started as did corn and barley with a low CEC, but instead of quickly rising to a peak and then dropping to a low value, the CEC rose slowly and attained a value at 3 weeks higher than that of corn and barley. Once the CEC values of beans surpassed that of corn and barley they remained higher. The 1 to 6 cm. section had the highest values followed by decreasingly lower CEC values for the 5 cm. sections obtained further from the apex of the root. At selected ages the 1 cm. bean root sections had CEC values, although higher, in line with those obtained for the larger 5 cm. sections.

CEC values obtained for the 1 cm. PI and Hawkeye soybean root sections were higher than those of corn and slightly higher than those of beans. The 1 to 2 cm. section had the highest CEC values as in the beans and corn.

A study of adsorption and sorption of iron by excised corn root sections was performed with the aid of the radioisotope Fe^{59}.

It was found that iron was adsorbed and sorbed along the entire length of the roots studied. In the case of corn root sections the greatest amount of iron was adsorbed in the 1 cm. sections with the highest CEC. With the exception of the tip 0 to 1 cm. section, the other bean root segments with the highest CEC adsorbed the greatest

amount of iron. For no apparent reason the 0 to 1 cm. section had the highest adsorption of iron, but did not have the highest CEC.

The CEC values of all corn root sections dropped off with age. This was accompanied by a decreased adsorption of iron. The rise in CEC values of bean root sections with age was accompanied by an increase in adsorbed iron.

No general pattern of iron sorption with section of root or CEC was found. There was, however, in both corn and beans less sorption by root sections from older plants as well as by sections obtained from older areas of roots regardless of plant age.

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APPENDIX

Table 8. Summary of CEC values obtained for 5 cm. root sections of KY7 corn in the age study (Section I)

Root Section (cm.)	Replicate	Age (days) 5	7	9	10	11	12	13	14	16	17	20	22	25	28
1 to 6	1	52	53	47	66	102	66	61	57	39	27	36	29	30	--
	2	57	51	49	60	96	64	67	54	40	29	39	30	33	--
	3	48	46	54	56	88	65	61	51	44	33	40	26	37	--
	4	47	50	46	62	78	49	61	62	37	15	33	35	28	--
6 to 11	1	21	24	27	40	44	36	36	47	41	33	28	26	27	25
	2	27	27	25	42	41	33	34	48	39	37	36	33	26	24
	3	19	22	21	47	46	19	17	41	36	31	22	28	31	31
	4	21	27	23	39	41	56	37	48	56	35	30	21	28	32
11 to 16	1	--	16	17	29	37	27	50	33	--	22	26	21	--	20
	2	--	14	19	26	35	29	39	34	--	19	31	21	--	17
	3	--	17	17	21	34	31	37	33	--	24	34	17	--	24
	4	--	13	15	24	38	9	34	36	--	7	29	17	--	31
First 5 cm. formed	1	--	--	16	21	16	17	21	27	24	11	17	12	15	--
	2	--	--	17	15	17	17	22	24	26	12	14	14	14	--
	3	--	--	19	16	21	20	29	26	22	10	16	11	12	--
	4	--	--	12	20	10	10	12	19	24	7	13	15	15	--

Table 9. Summary of CEC values obtained for 5 cm. root sections of Atlas barley (Section I)

Root Section (cm.)	Replicate	Age (days) 5	7	9	11	14	16	21	28
1 to 6	1	56	49	60	66	49	43	34	29
	2	51	57	62	63	41	39	30	29
	3	52	51	57	69	42	36	37	30
	4	49	31	57	58	52	42	35	28
6 to 11	1	--	43	47	47	45	27	27	21
	2	--	41	49	41	46	25	23	20
	3	--	46	43	44	38	29	26	17
	4	--	30	37	44	31	31	40	18
11 to 16	1	--	--	31	37	42	25	27	19
	2	--	--	30	32	41	23	21	17
	3	--	--	24	30	37	27	20	16
	4	--	--	27	25	44	29	20	12
First 5 cm. formed	1	--	--	15	16	15	14	14	12
	2	--	--	19	17	14	14	16	15
	3	--	--	17	16	16	13	13	14
	4	--	--	9	19	15	15	13	15

Table 10. CEC values obtained for 5 cm. root sections of Great Northern beans in the age study (Section I)

Root Section (cm.)	Replicate	Age (days) 10	11	14	20	42
1 to 6	1	52	30	46	53	97
	2	46	37	42	52	87
	3	37	27	56	60	88
	4	33	34	32	55	80
6 to 11	1	--	27	29	46	66
	2	--	21	22	47	65
	3	--	26	30	31	47
	4	--	30	43	36	78
11 to 16	1	--	--	26	29	42
	2	--	--	22	26	44
	3	--	--	24	19	39
	4	--	--	28	42	47

Table 11. Summary of CEC values obtained for 1 cm. root sections of KY7 corn, Great Northern beans, Hawkeye and PI soybeans (Section II)

Root Section (cm.)	Replicate	Corn Age (days) 10 to 12	Corn Age (days) 21	Corn Age (days) 35	Beans Age (days) 21	Beans Age (days) 35	Soybeans Hawkeye Age (days) 35	Soybeans PI Age (days) 35
0 to 1	1	46	64	47	46	127	89	119
	2	44	67	45	44	121	90	108
	3	51	68	41	41	126	77	111
	4	39	61	51	57	114	96	102
1 to 2	1	237	119	109	124	139	141	166
	2	221	121	111	121	140	147	167
	3	227	117	107	124	132	131	151
	4	247	95	85	123	141	137	172
2 to 3	1	139	89	56	91	79	140	109
	2	141	81	53	90	72	131	117
	3	129	92	51	76	71	126	101
	4	147	86	56	99	94	127	109
3 to 4	1	77	80	52	67	86	120	82
	2	71	71	54	62	87	109	86
	3	76	71	59	59	81	106	92
	4	72	90	79	64	86	105	96
4 to 5	1	30	36	41	40	65	57	97
	2	29	37	36	41	66	58	88
	3	31	41	34	39	71	66	86
	4	38	34	29	32	54	55	97

Table 12. Summary of Fe* adsorbed and sorbed by various root sections of KY7 corn at various ages (Section III)

Root Section (cm.)	Replicate	Age (days) 10 to 12	Age (days) 35	Age (days) 10 to 12	Age (days) 35
		Fe* adsorbed		Fe* sorbed	
		cpm			
0 to 1	1	428	47	752	622
	2	409	42	761	641
	3	401	71	773	658
	4	426	40	754	661
1 to 2	1	509	51	2683	1376
	2	547	52	2441	1384
	3	541	47	2611	1298
	4	547	62	2625	1466
2 to 3	1	442	90	3581	1407
	2	439	61	3453	1486
	3	411	53	3401	1592
	4	440	76	3373	1483
3 to 4	1	480	58	3492	1631
	2	487	51	3497	1647
	3	481	40	3560	1634
	4	468	63	3619	1636
4 to 5	1	401	71	2560	1381
	2	424	54	2593	1397
	3	459	48	2618	1380
	4	400	51	2617	1386

Table 13. Summary of Fe* adsorbed and sorbed by various root sections of Great Northern beans at various ages (Section III)

Root Section (cm.)	Replicate	Age (days) 12 to 14	Age (days) 35	Age (days) 12 to 14	Age (days) 35
		Fe* adsorbed		Fe* sorbed	
		cpm			
0 to 1	1	644	531	6396	5721
	2	601	547	6382	5727
	3	597	541	6471	5764
	4	578	509	6351	5700
1 to 2	1	290	314	7527	5990
	2	231	301	7523	5989
	3	257	316	7581	5978
	4	294	369	7469	6007
2 to 3	1	231	260	7982	6242
	2	236	279	7890	6109
	3	257	266	7997	6251
	4	224	247	8115	6350
3 to 4	1	277	281	7301	6562
	2	271	294	7342	6551
	3	242	277	7311	6558
	4	302	280	7306	6541
4 to 5	1	246	286	7778	6974
	2	247	285	7772	6901
	3	201	270	7789	6967
	4	270	243	7765	7050

Table 14. Summary of Fe* adsorbed and sorbed on excised KY7 corn root sections under varying times in Fe* and KCl solutions

Time in 0.05 N KCl Solution	Type of Fe* associated with the root	Time in Fe* solution (minutes) 1/2	1	2	5	10
(minutes)		cpm				
1/4	Adsorbed	237	307	317	327	340
		241	309	342	303	301
		221	314	286	333	322
1/4	Sorbed	442	691	761	764	1071
		463	702	752	771	1060
		454	695	797	778	1097
1/2	Adsorbed	446	457	472	472	497
		442	426	406	477	481
		438	479	517	476	489
1/2	Sorbed	439	663	967	1001	966
		451	640	901	916	979
		472	641	916	927	986
2	Adsorbed	466	468	445	451	440
		443	457	492	490	501
		456	452	491	493	493
2	Sorbed	498	797	931	947	1014
		490	797	901	937	960
		476	782	916	936	954