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¹ See for instance Glocker, R., *Zeit. Phys.*, **77**, 653-675 (1932).

² Collins, G. N., and Maxwell, L. R., *Science*, **83**, 375-376 (1936); Maxwell, L. R., *Phys. Rev.*, **51**, 375 (1937).

³ For the design used see Taylor, L. S., and Singer, G., *Radiology*, **15**, 637-646 (1930).

CONTACT EFFECTS BETWEEN PLANT ROOTS AND SOIL COLLOIDS

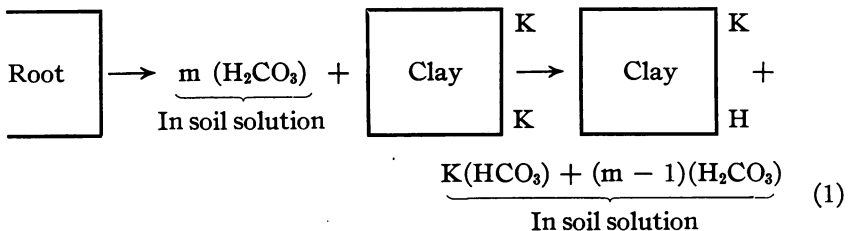
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Introduction.—The prevailing theories of mineral absorption by plants from soils are based on the concept of the *soil solution*. They postulate that a nutrient element must be an integral part of the soil solution before it can be taken up by plant roots. An ion is said to be in the soil solution when it is detached from the solid phase and can diffuse freely. It closely follows the movements of the liquid phase. Essentially, the soil solution is identified with the nutrient solution of the plant physiologist.

Equation (1) schematically illustrates the action of plant roots in soils as visualized by the soil solution theory.



The roots excrete carbonic acid into the liquid phase surrounding the soil particles. The H ions replace K from the surface of soil colloids and the resulting potassium bicarbonate is now ready for intake by roots.

In this paper an additional mechanism of mineral intake by plants from soils is proposed. It is based on the phenomenon of ion interchange existing between two surfaces which are in contact.

Theory of Contact Exchange.—Colloidal clays are negatively charged and possess high capacities for cation adsorption. The cations on the surface of the colloidal particles are not held rigidly. As a result of thermal agitation the ions oscillate and, at times, may be at considerable distances from the surface; but they remain in the field of force emanating from the colloid. Although the ions are surrounded by water molecules, they are not in solution in the sense that they can diffuse freely. The cations are under conditions of constraint and follow closely the movements of the colloidal particle to which they are attached.

These surface cations may be freed by exchange and then become an integral part of the intermicellar liquid or soil solution. According to the kinetic theory of ionic exchange¹ release may occur when a replacing ion enters the oscillation space of the adsorbed cation, as illustrated in figure 1. This process forms the basis for the mechanism represented by equation (1).

Conceivably, ionic exchange might also occur if two oscillation spaces overlap. This process may take place between neighboring ions on the



FIGURE 1

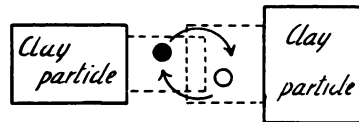


FIGURE 2

same surface and gives rise to the phenomenon of surface migration of ions. On the other hand if two separate colloidal particles approach so closely that the oscillation spaces interpenetrate, conditions for *contact exchange* between the two different particles exist as shown in figure 2. In this case the reaction as such is independent of the nature of the intermicellar liquid or soil solution. To use a picturesque expression one might say that the ions do not enter the soil solution *per se* but, in the moment of contact, jump directly from one particle to another.

The above considerations refer to ion transfer between particles of equal sign of any colloidal system. If roots with negative surfaces are immersed in colloidal clay suspensions (negative particles) there is good reason to believe that contact exchange might enter into play. Nutrient cations adsorbed on clay particles could thus become attached to plant roots directly, rather than by way of the soil solution. Since contact exchange involves a mutual transfer of ions, it follows that for every cation gained by the root an equivalent number of ions must leave the root surface and be transferred to the clay. For this reason we must distinguish between *contact intake* and *contact depletion*, as depicted in figures 3 and 4.

The experiments presented in this paper were designed to search for the

existence of contact phenomena between plant roots and colloidal clay particles. All efforts were concentrated on the phenomenon of contact depletion which is a particularly striking one, since the soil solution theories do not operate with the concept of depletion of roots. In this first paper data on the element potassium only will be reported.

Experimental Technique.—All experiments were conducted with barley plants of the Sacramento variety. They were grown according to the method of Hoagland and Broyer² and were used when they were three weeks old and about 18 inches high. The following types of systems were investigated.

(a) *Excised Roots.* About 100 grams of fresh roots were immersed in three liters of solution and aerated to insure optimum conditions for metabolism (Hoagland and Broyer²).

(b) *Decapitated Plants.* The shoots were cut off $\frac{3}{4}$ inches above the seed hull. Only the roots were dipped into the solution which was contained in shallow Pyrex trays.

(c) *Entire Plants.* The plants were left undisturbed, and roots and shoot were analyzed separately.

In all experiments listed under (a), (b) and (c) the roots were left in the solutions for a period of 10 hours. The loss of K was ascertained by analysis of the plant material using the cobaltinitrite method.³

(d) *Experiments with Radioactive Potassium.* The root systems of entire plants were kept for a few hours in KNO_3 solutions containing radioactive K. As soon as the shoot had accumulated substantial amounts of the radioactive element, the plants were transferred to the desired solutions. The outgo of K was determined by radioactive analysis of the solutions (Geiger counter).

Behavior of Roots in Distilled Water.—At the outset it was necessary to determine the loss of K when roots were placed in distilled water. For excised roots the data given in the table below are representative. The K content of the root is expressed as milliequivalents of K per 100 g. of dry roots. In all cases the losses are small and within experimental error. Special attention should be called to the last two rows of the table giving data for roots continuously leached for 10 hours with distilled water at a rate of ten gallons per hour. Nevertheless, the roots maintained their potassium level.

DRY WEIGHT OF ROOTS (168 PLANTS)	K CONTENT OF ROOTS M. E./100 G.	DIFFERENCE, PER CENT	REMARKS
3.66	43.1	...	Untreated
3.76	42.5	-1.4	In 3 liters H_2O
3.81	42.3	-1.9	In 3 liters H_2O
3.99	42.2	-2.1	In 100 gallons H_2O
3.55	41.4	-4.0	In 100 gallons H_2O

Similar tendencies were observed for plants which were allowed to accumulate radioactive K and then were kept in distilled water (7 plants in 400 cc.) for 4-7 hours. The radioactivity of 25 cc. of water corrected for background and radioactive decay and expressed in terms of "counts per minute" recorded by the Geiger counter is as follows:

$$\text{H}_2\text{O} \text{ (3.72 hour period)} = 8.1 \pm 3.82$$

$$\text{H}_2\text{O} \text{ (6.53 hour period)} = 6.6 \pm 5.36$$

The loss of radioactive K is small, less than 0.17 per cent and is statistically not significant. Evidently the low salt roots under investigation have a pronounced capacity to retain potassium against distilled water.

Behavior of Roots in Salt Solutions.—Since clays carry adsorbed cations, particularly Na, NH_4 , Ca or Mg, the question naturally arises whether these ions *per se* exert some specific influence on the condition of the root in relation to its power of retention of potassium. Accordingly, excised roots were kept for 10 hours in three liters of the following solutions containing 3-5 milliequivalents per liter: NaCl, NaHCO_3 , NH_4HCO_3 , CaCl_2 and MgCl_2 . In all cases the loss of K was small and did not exceed 4 per cent, which is still within experimental error. A HCl solution which was maintained at pH = 4.1 lowered the K content of the root by 5.1 per cent, a value which probably is significant.

A different picture is revealed by the more sensitive radioactive technique applied to entire plants. Their roots were kept for 11 hours in 900 cc. of various electrolyte solutions containing 5 milliequivalents of cations per liter and, in each case, 0.5 milliequivalents CaCl_2 . The following counts above background were obtained on 25 cc. of solution (background = 19.8 ± 1.62):

H_2O	=	8.9 \pm 7.00	KCl	=	42.8 \pm 9.78
LiCl	=	-6.9 \pm 7.22 ⁴	KNO_3	=	47.2 \pm 9.50
NaCl	=	-11.5 \pm 7.34	K_2SO_4	=	40.4 \pm 9.78
KCl	=	62.5 \pm 10.5	KH_2PO_4	=	47.1 \pm 10.80
NH_4Cl	=	188.8 \pm 17.7	KHCO_3	=	35.7 \pm 10.67
HCl	=	219.4 \pm 11.75			

A lyotropic series of monovalent cations for the removal of radioactive K from roots is indicated. The values for H_2O , LiCl and NaCl fall within the variability of the background (cosmic rays) and are not significant. In the cases of NH_4Cl and HCl the relatively high K outgo may have been in part a consequence of injurious effects of high electrolyte concentrations. A corresponding set with K salts (3.0 milliequivalents per liter) showed that inorganic anions which are common to nutrient solutions exerted no specific influence. The counts from systems containing MgCl_2 , CaCl_2 , SrCl_2 or BaCl_2 did not exceed the background. Regarding the actual

amounts of K involved, no definite figure can be given, except that the minimum amount of K lost by the roots is 0.000213 milliequivalents per 25 cc. per 100 counts.

Behavior of Roots in Colloidal Clay Suspensions.—The suspensions used in this study were of bentonite clay and of Yolo clay, both consisting of the common clay mineral montmorillonite. The bentonites were electro-dialyzed and then converted into the desired basic clays by addition of hydroxides, according to the equation $H\text{-clay} + NaOH = Na\text{-clay} + HOH$. The Yolo clays were subjected to leaching with neutral salts. The cation adsorption capacity (base exchange capacity) was 100 milliequivalents per 100 g. for the bentonites and 55 milliequivalents per 100 g. for the Yolo colloids as determined by the ammonium acetate method.

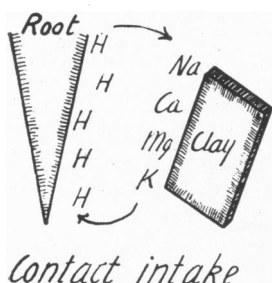


FIGURE 3

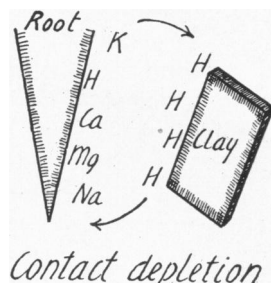


FIGURE 4

If excised roots are immersed in H or Ca-H bentonite suspensions for ten hours they suffer heavy losses of K as seen from the following data:

SYSTEM	CLAY CONCENTRATION, PER CENT	INITIAL pH OF SUSPENSION	K IN ROOTS M. E./100 G.	DIFFERENCE DUE TO COLLOID, PER CENT
H ₂ O	45.9
H-bentonite sol	3.97	3.05	4.7	-89.8
H-bentonite flakes	5.17	3.70	34.3	-26.0
K-H-bentonite sol	0.83	4.90	59.0	+28.5
Ca-H-bentonite sol	0.48	5.65	37.0	-19.4

The roots which lost 90 per cent of their total potassium showed indications of injury. From K-H-bentonite the roots accumulate K but lose Ca to the extent of 22.2 per cent. From Ca-H-clay they take up Ca ions (6.4 per cent) but lose K. The intake and outgo of nutrient ions is, therefore, of a differential nature. Coarse suspensions (flakes) are less effective than highly dispersed sols, as would be expected if contact phenomena are involved.

Furthermore, if excised roots are separated from H-bentonite suspensions (pH = 3.58) by a membrane which permits easy passage to ions but bars colloidal particles from contact with roots, no losses of K occur.

Likewise, if excised roots are suspended in a positive iron hydroxide sol (0.33 per cent) the lowering of the K level of the roots amounts to only 4.4 per cent. This is in harmony with the contact exchange theory according to which the negative barley roots⁵ should not transfer cations to positive colloids.

Experiments with plants which were decapitated $\frac{3}{4}$ inches above the base of the shoot fully corroborate the results obtained with excised roots, as shown in the following table:

SYSTEM	CLAY CONCENTRATION, PER CENT	INITIAL pH OF SUSPENSION	REDUCTION OF K CONTENT OF ROOTS, PER CENT
H-bentonite	0.53	3.85	26.8
Na-bentonite	0.48	7.35	14.8
NH ₄ -bentonite	0.41	7.25	32.6
Ca-bentonite	0.31	7.40	0.9

It appears that the nature of the adsorbed cation, rather than the pH of the suspension regulates the magnitudes of the K extraction by the colloidal particles; Ca-clay, in the concentrations used, did not influence the K status of the root systems.

Turning to radioactive experiments, the clay sols were compared with salt solutions, both systems containing equal amounts of cations. For 7 plants in 900 cc. liquid (5.0 milliequivalents cation + 0.5 milliequivalents CaCl₂ per liter) the following counts above background were obtained from 25 cc. solution after a contact period of 53 hours:

$H_2O = 7.1 \pm 6.45$	
$NaCl = 4.2 \pm 6.41$	$NH_4Cl = 668 \pm 49.8$
$Na\text{-Yolo colloid} = 606 \pm 92.5$	$NH_4\text{-Yolo colloid} = 1044 \pm 62.2$

Again the colloidal solutions are more effective than the true solutions, particularly in the case of the Na systems. With an improved technique of counting, the following measurements were made on divalent systems (2.2 milliequivalents cations per liter) which had 7 plants in 400 cc. solution for a period of 3.7 hours (counts above background, on 25 cc. solution):

$H_2O = 8.1 \pm 3.82$	$CaCl_2 = 11.3 \pm 3.68$
$MgCl_2 = 3.3 \pm 4.06$	$CaCO_3 = 17.0 \pm 3.50$
$Mg\text{-Yolo colloid} = 109 \pm 6.44$	$Ca\text{-Yolo colloid} = 66.3 \pm 3.81$

The greater efficiency of the clay systems as compared with the chloride salt solutions for extracting radioactive K from the roots is beyond doubt.

The influence of salt concentration and clay concentration on the removal of radioactive K from roots is illustrated in figure 5. The comparisons include KCl, CaCl₂, K-Yolo and Ca-Yolo colloids. Two features are outstanding. First, the effects of monovalent cations exceed those of the divalent cations; second, the clay systems uniformly give higher counts

than the salt solutions. These data convincingly prove the importance of root-colloid effects. The results obtained with the radioactive technique fully substantiate the observations made with excised roots and decapitated plants.

Injury Tests.—The root systems of entire plants were immersed in H-bentonite sols (0.16 per cent) until they had lost 20.0 per cent of their total potassium. When these roots were transferred to nutrient solutions and

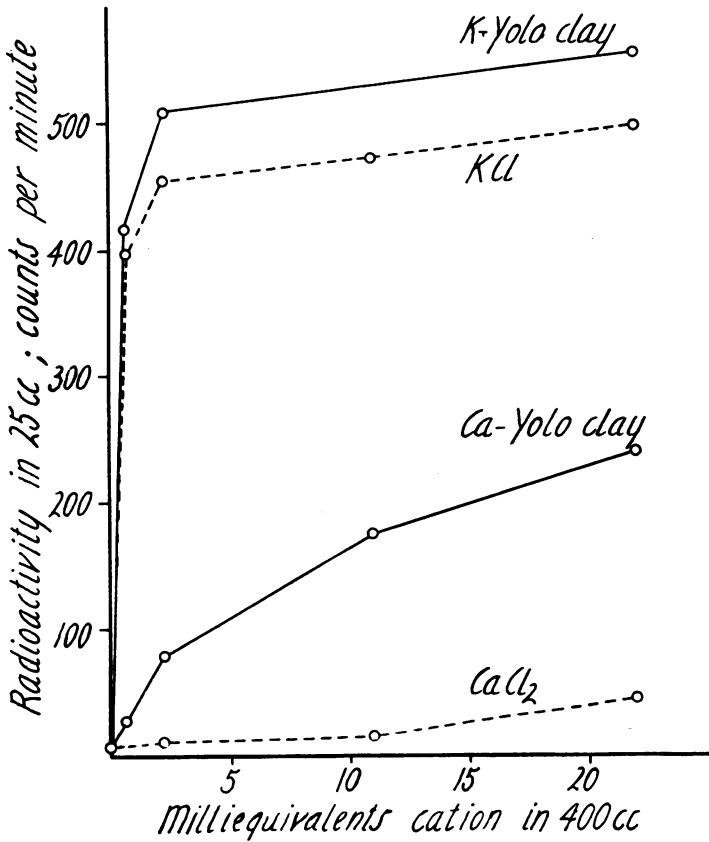


FIGURE 5

kept there for 12 hours they accumulated K to the extent of 153 per cent of their original K content. Apparently the clay treatment had not impaired the capacity for salt accumulation; in fact, the roots which had been in the bentonite sol proved to be just as efficient absorbers as the control roots which were not in contact with the clay.

A set of radioactive K roots (84 plants) were kept in a K-Ca-clay suspension for six hours, and during this time they continuously lost large

amounts of radioactive K. When these plants were transferred to distilled water the outgo of radioactive K immediately fell to such small magnitudes that the counts of the water did not exceed those of the background. It must be concluded that if any root injury occurs it can hardly be attributed to contact as such; rather it must be considered a consequence of resulting disturbances of the electrolyte balance within the plant system.

New Aspects of Plant Nutrition.—The barley plants grown by the technique referred to in this article possess an inherent capacity for pronounced accumulation of various nutrient cations. The radioactive tests reveal that during intake there occurs, simultaneously, a release of nutrient cations to the surrounding medium.

Particularly striking are the observations with radioactive K roots immersed in KCl or K-clay (figure 5). Potassium from the nutrient medium moves into the plant whereas K contained in the root is migrating out. In the case of 10 per cent K-clay (figure 5) the roots transferred about 10 per cent of their radioactivity to the clay particles.

Quantitative insight is gained from the following crucial experiment. Eighty-four radioactive plants were placed for 5 hours in a K-Ca-bentonite suspension (0.35 per cent). The roots weighed 4.51 g. (oven dry) and contained initially 1.685 milliequivalents K. At the end of the experiment they contained 2.840 milliequivalents K, a gain of 1.155 milliequivalents or 68.3 per cent. This latter value represents only the net intake. Actually the roots must have absorbed larger amounts of K because they simultaneously yielded at least 0.114 milliequivalents K to the clay, as indicated by the outgo of radioactive potassium.

In view of these findings, our concepts of the mechanism of mineral absorption by plants must be modified and extended. The results show that the intake of ions is not an uni-directional process; ions of the same species may move into the root and out of the root at the same time. The outgo is especially pronounced when the roots are in contact with colloidal systems. Accumulation and depletion are only net effects of ionic movements.

Acknowledgments.—The authors are indebted to Professor D. R. Hoagland for his interest and valuable suggestions, to Professor E. O. Lawrence, Director of the Radiation Laboratory, for supplying radioactive potassium and to Mr. A. D. Ayers for technical assistance.

A detailed account of the experiments will be published in *Soil Science*.

¹ Jenny, H., *Jour. Phys. Chem.*, **40**, 501 (1936).

² Hoagland, D. R., and Broyer, T. C., *Plant Physiol.*, **11**, 471 (1936).

³ Hibbard, P. L., and Stout, P. R., *Jour. Assoc. Offic. Agric. Chem.*, **26**, No. 1, 137 (1933).

⁴ This negative value was obtained as follows: Ten readings of the background gave

a value of 19.8 ± 1.62 . Ten readings of 25 cc. of LiCl solution gave a count of 17.7 ± 1.62 which is within the variability of the background. The difference, -2.2 ± 2.29 multiplied by the radioactive decay factor of 3.15 gives the tabulated value, -6.9 ± 7.22 .

⁵ That the roots are negative is indicated by measurements of streaming potentials, and moreover by the fact that positive particles of iron hydroxide strongly adhere to the root while negative clay particles do not show such a behavior. The dried, ground roots have a cation adsorption capacity of about 11 milliequivalents per 100 g. as determined by the ammonium acetate method.

ON LOCALLY CONNECTED SETS AND RETRACTS

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In the present Note we propose to summarize a few results on locally connected sets and retracts. For the definitions we refer the reader to an earlier paper.¹ By way of notation we designate here by LC^* , LC^{**} the types designated by LC , \overline{LC} , loc. cit. Likewise instead of *semi-singular* complex, we shall say *partial realization* of a complex. The comparison with the retracts (loc. cit., Theorem II) reads now: $LC^* = ANR$, $LC^{**} = AR$.

A closed locally finite (with finite stars) simplicial geometric complex \mathfrak{R} with countable elements $\sigma^1, \sigma^2, \dots$ is said to be *regular* whenever $\text{diam. } \sigma^i \rightarrow 0$ with $1/i$. Similarly a partial or full realization L of \mathfrak{R} on a metric space \mathfrak{R} is *regular* whenever if ζ^i is the sum of the faces of σ^i already realized, $\text{diam. } \zeta^i \rightarrow 0$ with $1/i$. A continuous complex K which is the extension of L to \mathfrak{R} minus a finite closed sub-complex is said to be an *almost full realization* of \mathfrak{R} .

In the sequel \mathfrak{R} shall designate a compact metric space.

THEOREM 1. *N. a. s. c. for \mathfrak{R} to be LC^p is that every regular partial realization of a complex such as \mathfrak{R} , where $\text{dim } \mathfrak{R} \leq p$, may almost be extended to a full realization K of \mathfrak{R} . For LC^* the result is the same without dimensional restriction, and likewise for LC^{**} except that K must be a full realization.*

If we compare with Theorem I of our paper and the LC^* , LC^{**} definitions, we find that the ϵ , η conditions are replaced by the "structure" of the infinite complexes.

Let now \mathfrak{R} be a finite simplicial geometric complex and let U map \mathfrak{R} on \mathfrak{R} , thus giving rise to a continuous complex K on the latter. We assign to K the dimension of \mathfrak{R} . Let now A be a set on \mathfrak{R} and let it be mapped by W on the set A' of the same space. If there exists a mapping $V: A \rightarrow \mathfrak{R}$