WATER UPTAKE AND ROOT GROWTH AS INFLUENCED BY INEQUALITIES IN THE CONCENTRATION OF THE SUBSTRATE

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(WITH FIVE FIGURES)

Introduction

When a number of solutions of unlike concentration are presented at one and the same time either to an established or to a developing root system, questions follow as to whether water is withdrawn as rapidly from the concentrated as from the dilute regions and as to whether new roots extend themselves as readily in the regions of high salinity as in those of low salinity. The subject is of agronomic, as well as physiological, significance since the productivity of soils must be regarded as being contingent not only on their nutrient and water storage resources but also upon the readiness with which these resources can be utilized by plants.

A substantial diversity is customarily found in the salt concentrations of the soil solution within the root zone of single plants growing on irrigated lands. The data of table I, which are presented as an illustration, represent analyses of displaced soil solutions from samples collected in a sparingly irrigated but relatively permeable and well drained orchard soil. Conductivity measurements made on the solutions displaced from the separate one-foot horizons before combining them for analyses showed a greater variability than is here indicated; the variability in more heavily irrigated soils, however, is usually lower than that found in this instance. All of the

TABLE I

VARIABILITY OF CHLORIDE, SULPHATE, AND NITRATE CONCENTRATIONS (MILLEQUIVALENTS PER LITER) IN DISPLACED SOIL SOLUTIONS OF A WELL-DRAINED BUT SPARINGLY IRRIGATED ORANGE ORCHARD IN THE SIERRA MADRE FOOTHILL AREA OF SOUTHERN CALIFORNIA. SAMPLES WERE COLLECTED ON THE NORTHWEST AND NORTHEAST SIDE OF EACH OF TWO TREES

DEPTH	TREE 30, ROW 22						TREE 36, ROW 22					
	SO_4		Cl		NO_3		SO_4		Cl		NO_3	
	NW	NE	NW	NE	NW	NE	NW	NE	NW	NE	NW	NE
feet	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*	*m.e.*
0– 3	2.3	3.3	1.2	2.4	4.5	5.0	9.1	2.1	1.6	1.1	2.3	2.0
3– 6	11.8	36.6	1.8	25.2	0.9	4.8	53.3	40.3	13.1	12.1	9.6	8.1
6–10	17.2	40.4	4.2	81.6	4.1	10.5	43.5	42.6	47.9	16.5	25.7	10.2

samples were wetted to approximately the moisture equivalent before displacement.

The experimental work here reported upon includes a series of tests conducted in water cultures with tomato and corn plants. The root systems of these plants were divided between solutions that differed in concentration and in the character of the added salts. The effects of the treatments were measured in terms of root growth and water uptake.

Review of literature

The review of literature that follows is confined to papers concerned primarily with the cross transfer of water and solutes in plants. The problem under consideration, however, bears also upon broader fields of inquiry that concern some of the forces involved with water uptake and with some of those governing the growth of roots.

Gile and **Carrero** (**8**) found the total amount of nitrogen or phosphorus absorbed by rice plants having half of their roots in complete nutrient solution and half in solutions deficient in these elements was 76 per cent. of that of plants having all roots supplied with complete nutrient solution. In a subsequent paper (**9**) they reported a lesser growth of the portion of the root system of corn plants which extended into solutions deficient in nitrogen, phosphorus, or potassium. Their solutions were all dilute (about 5 m.e. of total bases per liter), so there could have been but little difference in osmotic concentrations. **McMurtrey** (**14**) using a similar technique, reported an unilateral development of the leaves of tobacco plants with roots divided between complete nutrient and element-deficient nutrient solutions. He mentioned, and one of his photographs shows, increased root growth when calcium (previously omitted) was added to one of the two solutions supplied to a single plant.

Auchter (**1**) applied nitrate of soda on one side of field trees and concluded that under normal conditions mineral nutrients absorbed by roots on one side are translocated to and used by the trunk, limbs, and leaves above them and that foods manufactured by one side are used or stored on that side or translocated to the roots of the same side. The behavior of trees with half of their roots severed prompted the conclusion that water can move laterally in trees without much difficulty. **Furr** (**7**), finding the volume of lemon fruits to be independent of position over cut and uncut roots, also concluded that there was a ready cross-transfer of water throughout old lemon trees. **Auchter** and **Schrader** (**2**), in experiments continued for two years, thought there was little if any cross transfer of carbohydrates from sun-exposed to cloth-enclosed sides of apple trees. **Miller** (**15**), has reviewed a series of papers showing a tendency toward increased root development in fertilized portions of soils. **Caldwell** (**4**) reports an asymmetric development of the fleshy root of the Swede turnip when leaves were removed from one side. The roots below the defoliated side of Coleus plants (**5**) grew less than the roots under the foliated side. Experiments (**1, 5**) on plants with roots divided between rich soil and sand have added support to the foregoing conclusions. NIXON[1] has found that date fruits on strands subtended below, and in line with, a notch cut in the fruit stalk that severed about 50 per cent. of the vascular system increased in dry matter during the summer; this indicates some cross-transfer of manufactured foods from the unsevered to the severed side of the stalk.

Methods

Both corn and tomato plants were used for the experiments. The former was regarded a nearly ideal test plant since its vascularity is such as to largely preclude a unilateral development of the top or a differential accumulation of salt in the leaves of one side. It will be recalled that each leaf sheath of the corn plant encircles the stalk at the node from which it arises and that, owing to anastomoses, the nodal structures favor lateral distribution of constituents rising or descending through the vascular system. Anatomical studies of the vascular system of the potato would imply that some lateral distribution of solutes rising or descending in tomato shoots is likewise to be expected.

Lacquered rectangular metal cans with openings cut in one corner, or in the middle of one side of the top, large enough to admit a group of roots were used as culture vessels. These containers (figure 5) used in groups of two or four, were bound together in such a manner that portions of the root system of a single plant could be extended into each. Water was added to the cans through openings having screw caps. Gallon containers were used in experiments 1 and 2, and quart containers in the other experiments.

The plants were grown to a height of 15 to 25 cm. in nutrient solutions in preparation for experimental use and the separation of roots into groups. After dividing the roots into 2 or 4 equal groups, trimming when necessary, they were dusted heavily with carbon black to facilitate a differentiation at the end of the experimental period between the original roots and those subsequently developed.

The plants were fastened in place with cork and cotton mountings, and the roots at the point of division were separated by cork wedges 1 cm. tall that rested on the edges of the cans. Further, to make unlikely the movement of solution from one container to another by wick action, the levels of the solutions were not brought nearer than 1.5 cm. to the tops of the containers. A can with a similar opening was set up in conjunction with each experiment to measure direct evaporation. The loss from this container has been deducted from all results to give net water-uptake values.

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[1] R. W. NIXON, unpublished data.

The base nutrient solution contained calcium nitrate, potassium nitrate, magnesium sulphate and potassium dihydrogen phosphate in concentrations of 5, 5, 2 and 1 millimoles per liter respectively (HOAGLAND'S solution). This solution was used in the foregoing concentration and in fractional and multiple concentration both alone and in conjunction with added chloride and sulphate salts. These latter salts were added 50 per cent. as m.e. of sodium, 25 per cent. as magnesium, and 25 per cent. as calcium. All solutions contained, in addition to the foregoing, 1 p.p.m. of boron, 0.2 p.p.m. of zinc, and 0.5 p.p.m. of manganese. Iron was added in the form of tartrate or citrate as needed.

The freezing point depressions, $\Delta°$ C, and electrical conductance, $K \times 10^{-5}$, and other determinations of concentration on used solutions were always made after the containers had been restored to their initial weights by adding distilled water. Distilled water was added frequently throughout the experiments to replace transpiration losses. All of the experiments were conducted in a greenhouse. Only the fresh weights of roots are reported since the concentration of the solutions did not affect significantly the percentage of moisture in the roots in those instances (experiment 3) when both fresh and dry weights were measured.

Results

EFFECT OF UNILATERALLY SUPPLIED SALTS ON ROOT GROWTH AND WATER UPTAKE. EXPERIMENTS 1 TO 7

In experiments 1 to 7, inclusive, the root systems of corn and tomato plants were divided between two or more solutions that differed in composition and concentration. The results of these experiments (tables II to V) are alike in showing a greater water-uptake from, and a greater root growth in, the solutions of low concentration than in those of high concentration.

In experiment 1 with corn (table II) nearly twice as great a weight of roots developed in a solution with a trace of chloride as in a solution with 10 m.e.; little or no root growth resulted in solutions with 50 and 250 m.e. of chloride (fig. 1). The effect on water-uptake was also marked. The solution with 250 m.e. of chloride, if it were the only one supplied, would probably be too saline for the growth of corn plants. This relation would not hold for 50 m.e. of chloride since corn plants on such solutions under similar conditions (**6**) made 62 per cent. as much total growth as in control solutions without chloride. The roots in the chloride solutions of those experiments were heavier relative to the weight of the shoots than in the control solutions.

Chloride determinations (table II) on the solutions at the beginning and end of experiment 1 indicate some movement of chloride through the roots into the solution that started with a trace of chloride.

In experiment 2, with a tomato plant, a significant reduction in water

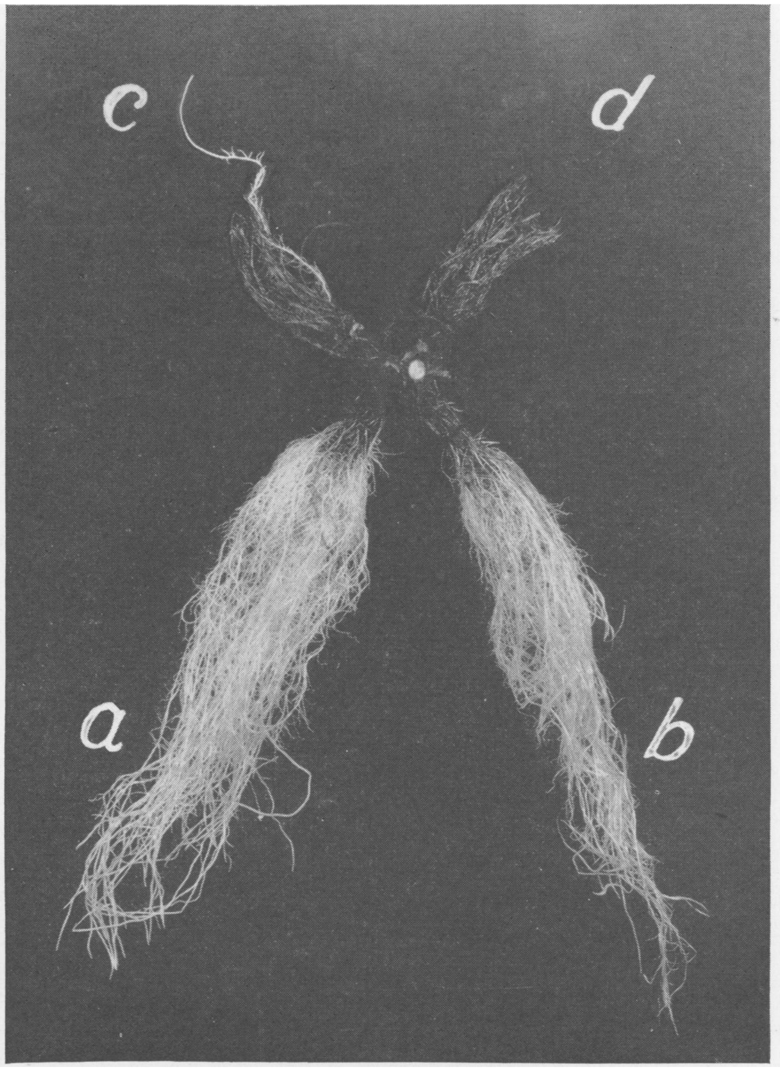

FIG. 1. The differential development of new roots of a corn plant 22 days after the initial roots had been divided between vessels containing in addition to the base nutrient solution: a, trace; b, 10 m.e.; c, 50 m.e.; and d, 250 m.e. of chloride. The roots on the plants at the start of the experiment were dusted with carbon black. Experiment 1.

uptake and a lesser development of roots resulted when the roots were supplied with 22.5 m.e. of chloride; the effects of 7.5 m.e. of chloride, however, were negligible (table I). In this as well as in subsequent experiments with tomatoes, the compact matting of the roots made it difficult to differentiate very accurately between the old and new ones.

TABLE II

Roots of corn and tomato plants divided between four solutions with different concentrations of chloride. Experiments 1 and 2

Container	Solution designation	$K \times 10^{-5}$ at 25° C.		Chloride per liter		New roots		Water uptake	
		Initial	End	Initial	End				
				m.e.	*m.e.*	*gm.*	*%*	*ml.*	*%*
Experiment 1. Corn plant in base solution with added chloride. Duration 22 days									
A	Trace Cl	220	210	0.10	2.14	8.8	63	908	66
B	10 m.e. Cl	320	298	10.17	9.69	5.1	36	348	26
C	50 m.e. Cl	705	691	48.21	47.50	0.1	1	53	4
D	250 m.e. Cl	2542	2486	254.0	244.0	0.0	0	55	4
Experiment 2. Tomato plant in base solution with added chloride. Duration 22 days									
A	Trace Cl	214	166	0.05	0.11	8.1*	31	820	35
B	7.5 m.e. Cl	291	241	7.46	7.07	8.2*	31	777	33
C	22.5 m.e. Cl	443	392	22.27	21.22	5.4	21	540	23
D	75 m.e. Cl	937	891	73.56	71.64	4.4	17	215	9

* The new and old roots in these containers were so badly matted together that it was impossible to differentiate very closely between them.

All of the original solutions of experiment 2 contained 15 m.e. of nitrate and 6 m.e. of potassium per liter. Measurements made at the end of the test showed that the concentrations in containers A, B, C and D had been reduced to 10.7, 10.9, 11.6, and 13.8 m.e. of nitrate, and to 4.2, 4.7, 4.9, and 6.2 m.e. of potassium per liter, respectively. It is probable that the greater number of roots in the solutions of lower concentration had as much to do with the

TABLE III

Corn roots divided between 4 solutions with the base nutrient and different concentrations of chloride. Duration 28 days.
Experiment 3, duplicate tests

Container	Solution designation	New solutions		End solutions $K \times 10^{-5}$ at 25° C.	New roots		Water uptake	
		Δ	$K \times 10^{-5}$ at 25° C.					
		°C.			*gm.*	*%*	*ml.*	*%*
Plant no. 1								
A	Trace Cl	0.016	215	55.9	16.5	33	2291	39
B	10 m.e. Cl	0.091	317	158.0	14.7	29	1941	33
C	20 m.e. Cl	0.123	420	280.0	11.6	23	1173	18
D	40 m.e. Cl	0.180	619	504.0	7.3	15	706	10
Plant no. 2								
A	Trace Cl	0.016	215	67.3	9.3	29	2062	37
B	10 m.e. Cl	0.091	317	222.0	8.7	27	1790	32
C	20 m.e. Cl	0.123	420	306.0	7.2	22	1090	18
D	40 m.e. Cl	0.180	619	502.0	7.2	22	827	13

greater uptake of these nutrient ions as did the lower concentrations of chloride, calcium, magnesium, and sodium.

Experiment 3 (table III) included duplicate tests with corn grown in solutions containing, respectively, a trace, 10, 20, and 40 m.e. of chloride. The plants showed depressed root growth and lower water-uptake from the successively stronger solutions. A relatively greater effect on water uptake than on root growth resulted (fig. 2).

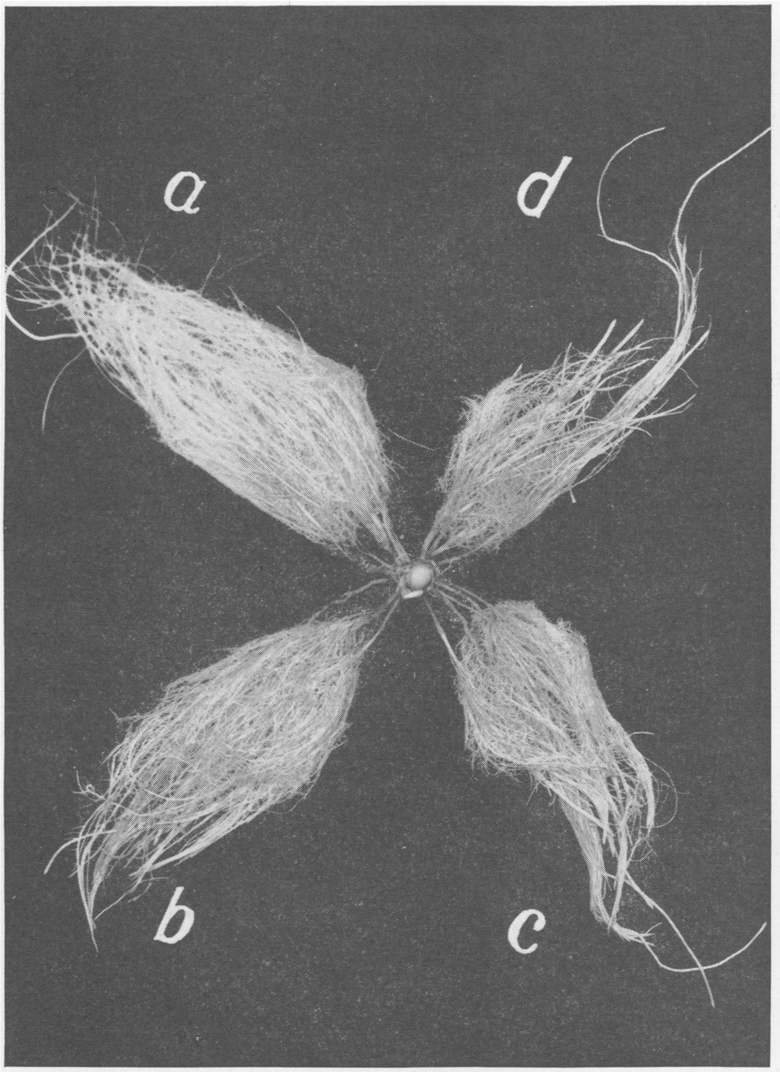

FIG. 2. Roots of a corn plant divided between solutions with: a, trace; b, 10 m.e.; c, 20 m.e.; and d, 40 m.e. chloride. Plant 1, Experiment 3.

Experiments 4 and 5 were conducted for the purpose of determining if sulphate would have an effect similar to chloride on root growth and water uptake. The chloride and sulphate concentrations were selected to give roughly similar differences in the osmotic pressures of the solutions compared. The resulting data (table IV) indicate no pronounced difference between the effects of chloride and sulphate salts at similar osmotic pressures.

TABLE IV

CORN PLANTS WITH ROOTS DIVIDED BETWEEN SOLUTIONS WITH ADDED CHLORIDE (EXPERIMENT 4), AND ADDED SULPHATE (EXPERIMENT 5)

CONTAINER	SOLUTION DESIGNATION	NEW SOLUTION		NEW ROOTS		WATER UPTAKE	
		Δ	$K \times 10^{-5}$ AT 25° C.				
		°*C.*		*gm.*	%	*ml.*	%
Experiment 4. Corn plant with roots in base nutrient with 2 chloride concentrations. Duration 13 days							
A	10 m.e. Cl	0.090	317	2.7	69	306	72
B	25 m.e. Cl	0.138	472	1.2	31	119	28
Experiment 5. Corn plant with roots in base nutrient with 2 sulphate concentrations. Duration 13 days							
A	20 m.e. SO_4	0.097	359	3.6	78	294	68
B	40 m.e. SO_4	0.150	561	1.0	22	139	32

TABLE V

CORN AND TOMATOES WITH ROOTS DIVIDED BETWEEN 3 × BASE NUTRIENT AND 0.5 × BASE NUTRIENT WITH ADDED CHLORIDE. EXPERIMENTS 6 AND 7

CONTAINER	SOLUTION DESIGNATION	NEW SOLUTIONS		NEW ROOTS		WATER UPTAKE	
		Δ	$K \times 10^{-5}$ AT 25° C.				
		°*C.*		*gm.*	%	*ml.*	%
Experiment 6. Corn plant with roots in concentrated base nutrient and dilute base nutrient plus chloride. Duration 13 days							
A	3 × base nutrient	0.157	583	1.8	51	146	54
B	0.5 × base nutrient plus 50 m.e. Cl	0.183	626	1.7	49	125	46
Experiment 7. Tomato plant with roots in concentrated base nutrient solution and dilute base nutrient solution plus chloride. Duration 17 days							
A	3 × base nutrient	0.167	599	4.1	45	435	53
B	0.5 × base nutrient plus 50 m.e. Cl	0.163	534	5.1	55	425	47

Experiments 6 and 7 (table V) were conducted to give further information on the question of whether the previously observed effects were the result of the action of specific ions or primarily reactions related to the total osmotic pressures of the solutions. In these experiments the behavior of corn and tomato plants was observed when their roots were divided between two solutions similar with respect to osmotic pressure but unlike in that one was concentrated base nutrient and the other dilute nutrient plus enough chloride to produce a similar total concentration. The effects of the two solutions were much alike with both corn and tomato. This finding may warrant the conclusion that osmotic relations are primarily involved but, if so, the fact should not be overlooked that nitrate was the principal anion (45 m.e.) in the 3 × base nutrient.

SEPARATION OF EFFECTS OF ROOT AREA AND OSMOTIC PRESSURE ON WATER UPTAKE

At the beginning of each of the foregoing tests the number of roots in the several solutions of an experiment were nearly the same whereas by the end of the experiments there were more roots in the dilute than in the concentrated solutions. Experiments 8 and 9 (table VI) were undertaken to obtain an appraisal of the effects of solution concentration on water uptake that would be independent of number of roots. The first of these experiments (number 8) was conducted in the same manner as those that had pre-

TABLE VI

DIFFERENTIATION OF EFFECTS OF NEW ROOT DEVELOPMENT AND OSMOTIC PRESSURES ON WATER UPTAKE. EXPERIMENTS 8 AND 9

CONTAINER	SOLUTION DESIGNATION	NEW SOLUTION		NEW ROOTS		WATER UPTAKE	
		Δ	K × 10^{-5} AT 25° C.				
		°C.		*gm.*	*%*	*ml.*	*%*
Experiment 8. Corn plant with roots in different concentrations of base nutrient solutions. Duration 13 days							
A	0.5 × base nutrient	0.025	113	3.6	62	451	76
B	3.0 × base nutrient	0.153	581	2.2	38	146	24
Experiment 9. Same as experiment 8 but positions of roots alternated between the two solutions every second day							
A	0.5 × base nutrient	0.025	113	......	......	319	65
B	3.0 × base nutrient	0.153	580	......	......	171	35

ceded it; in experiment 9, however, the positions of the roots in the two solutions were reversed each second day; *i.e.*, the roots in container A were placed in container B and vice versa. By thus alternating the two halves of the root system between the concentrated and dilute solutions it was possible to maintain essentially equal root areas in the two solutions throughout the experimental period. At the end of experiment 9 one group of roots weighed 32 and the other 36 grams; this is probably as close an agreement as could be expected when account is taken of the difficulties attached to dividing the roots of a plant at the beginning of a test period into two equal groups.

A three-fold difference in water-uptake resulted in experiment 8 where the combined effects of differences in root area and in solution concentration were represented. In experiment 9, however, where essentially equal root areas were presented in each of the solutions, there was approximately a two-fold difference in water uptake. This latter result, which can be regarded as representing the effect of solution concentration alone, will be considered further in the discussion and in figure 5.

ROOTS DIVIDED BETWEEN NUTRIENT SOLUTIONS AND DISTILLED WATER

In the three succeeding experiments, tables VII and VIII, the roots of corn and tomato plants were divided between distilled water and 2 × base nutrient. The situation thus created is obviously complex since it is well known that distilled water is injurious to plant roots. The question remained, nevertheless, as to whether the injury to roots would be of such a character as to lessen the rate of water uptake and also whether there would be enough movement of salts from the roots to the distilled water to permit some growth after several days had elapsed.

TRUE (**18**) has traced the development of views on the causes of injurious effects of distilled water on root growth from the observations of early physiologists, who thought the absence of nutrients was responsible, through the period when the ill effects were attributed to metals derived from stills. From his own work with lupine seedlings (**18**), he concluded that a causal connection between loss of electrolytes by roots and their falling growth rate was almost certain. Injury was not prevented in his experiments when sugar or sodium chloride was added to the solutions to give osmotic pressures equal to that of Potomac River water used as a control. Calcium chloride prevented injury. TRUE, referring to work of TRUE and BARTLETT, points out that Canada field pea seedlings made a fairly healthy growth in distilled water despite the loss of considerable quantities of electrolytes to the outer solution.

HIBBARD (**10**) found that a slow process of adjustment or acclimatization to distilled water fitted *Lupinus alba* seedlings to better growth than thrusting them directly into it. Finding that root growth was increased when the distilled water was changed 4 times daily, he concluded that the roots were injured because they secreted a substance toxic to themselves. Scarth (**17**) found that boiling distilled water in silica vessels to expel carbon dioxide changed the pH from 5.5 to 7.1 and reduced the toxicity to Spirogyra. The tests were made in covered beakers but mention is not made that air or light was thereby excluded and the pH of the distilled water after the algae had been in it for some hours is not given.

The water used in the present experiments was from a gas-heated Barnstead still and it was stored in tin-lined copper tanks. It was not redistilled and it is not known to what extent the carbon black on the roots adsorbed traces of copper or other metals.

As shown by table VII the roots of both corn and tomato made a better growth in the nutrient solution than in the distilled water and for the full duration of the experiment more water was taken up from the solution of higher concentration. During the first days of all three experiments, however, relatively more water was removed from the distilled water vessels (table VIII) than from 2 × base nutrient; thus indicating that the injury to the roots—whatever its cause or character—did not prevent what was apparently a normal uptake of water. Later, when new and actively grow-

TABLE VII

Corn and tomatoes with roots divided between distilled water and 2 × base nutrient. Experiments 10, 11, and 12

Container	Solution designation	New solutions		New roots		Total water uptake	
		Δ	K × 10^{-5} at 25° C.				
		°*C.*		*gm.*	%	*ml.*	%
Experiment 10. Two corn plants. Duration 34 days							
A	Distilled water	....	.45	4.3	11	588	12
B	2 × base nutrient	0.113	413.00	34.0	89	4126	88
Experiment 11. Two tomato plants. Duration 17 days. Stems not split							
A	Distilled water	....	.45	10.3	38	1175	42
B	2 × base nutrient	0.113	413.00	16.7	62	1605	58
Experiment 12. Two tomato plants. Duration 34 days. Stems split up about 5 cm.							
A	Distilled water	....	.45	3.8	9	2886	30
B	2 × base nutrient	0.113	413.00	39.0	91	6647	70

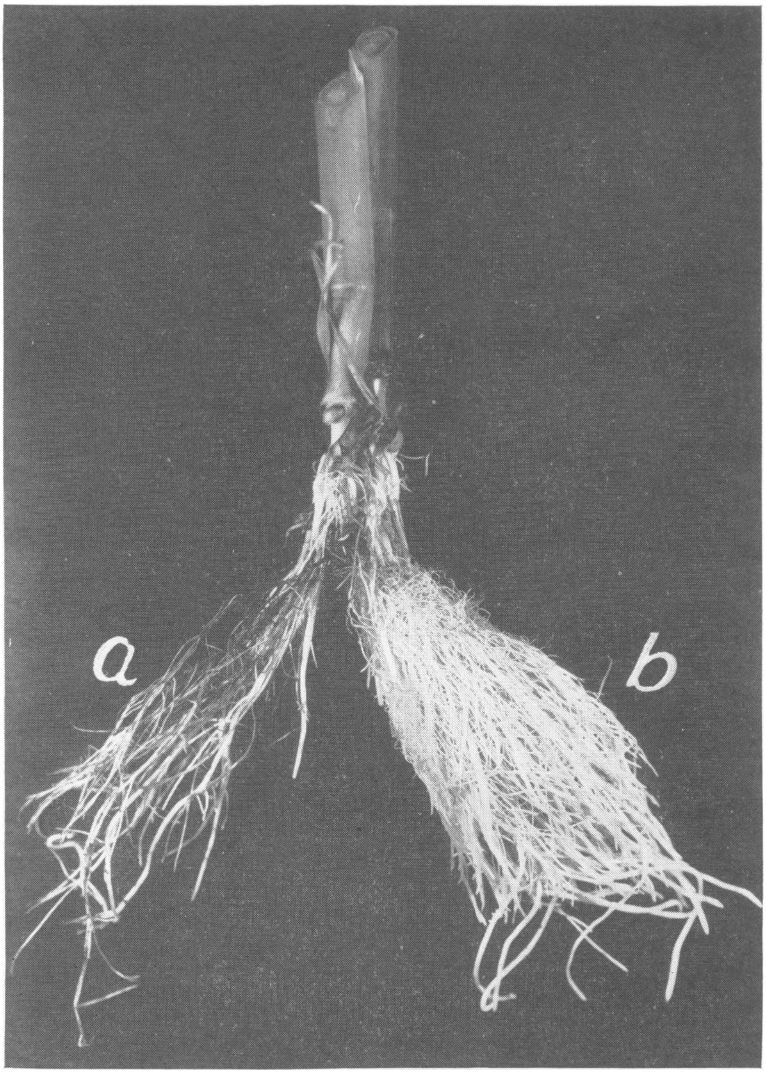

FIG. 3. Corn roots. a, in distilled water; b, in 2 × base nutrient.

ing roots had developed in the containers with nutrient solution, the rate of uptake from the nutrient solution exceeded that from the distilled water. The original roots constituted a greater proportion of final roots in these tomato experiments than in the corn experiment and relatively more water was taken up from the distilled water by the tomatoes than by corn (figs. 3 and 4).

There is substantial evidence (table VIII) in each of these three experi-

TABLE VIII

WATER UPTAKE BY PERIODS AND CONDUCTANCE OF USED SOLUTIONS AT END OF PERIODS. EXPERIMENTS 10, 11, AND 12

CONTAINER	SOLUTION DESIGNATION	WATER USE BY PERIODS				CONDUCTANCES OF SOLUTIONS REMOVED		
		0 to 3*	0 to 10	11 to 17	18 to 34	10th	17th	34th
		ml.	*ml.*	*ml.*	*ml.*			
		Experiment 10. Corn						
A	Distilled water	90	145	79	364	9.22	0.99	1.32
B	2 x base nutrient	40	167	470	3489	356.00	305.00	296.00†
		Experiment 11. Tomato						
A	Distilled water	190	590	585	....	6.64	0.96	....
B	2 x base nutrient	140	750	855	....	225.00	202.00	....
		Experiment 12. Tomato						
A	Distilled water	190	405	595	1886	10.70	1.56	6.85
B	2 x base nutrient	90	345	918	5384	350.00	205.00	232.90†

* Approximate since solutions were not removed from containers for measurement.

† This solution renewed on 31st day—conductance not recorded.

ments indicating the movement of solutes from the roots into the distilled water; the nature of the electrolyte so moved, however, was not determined. A conductance of 10×10^{-5}, such as was observed in the first period of both experiments 10 and 12, corresponds to about 1 m.e. of cations per liter.

Discussion and conclusions

WATER RELATIONS

Experiment 9 provides a suitable basis for discussion of the effect of solution concentrations on water uptake by divided root systems. It was found that 1.86 ml. of water was withdrawn from the nutrient solution with an osmotic pressure of 0.3 atm. for each 1 ml. of water withdrawn from the nutrient solution with an osmotic pressure of 1.8 atm. Inasmuch as the characteristics of the two halves of the root system remained equal throughout the test it may be possible to estimate the magnitude of a maintained tension in the water in the base of the shoot that would be necessary to satisfy both of the two pairs of values (table VI, fig. 5).

The forces peculiar to living cells and tissue are neglected in the calculations that follow and it becomes of interest for this reason to consider to what extent such omissions are justified. Guttation is believed in some

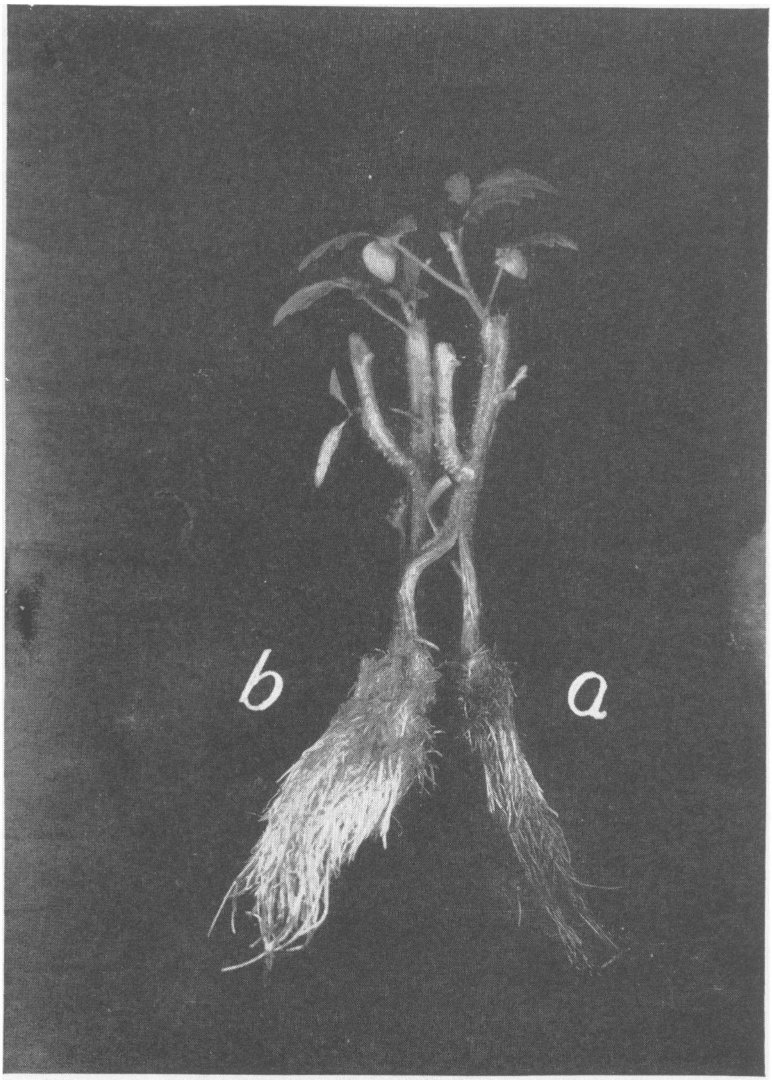

FIG. 4. Tomato roots. a, in distilled water; b, in 2 × base nutrient.

instances to represent glandular action; MASON and PHILLIS (**13**) have shown that the osmotic pressures of protoplasmic saps are greatly in excess of vacuolar saps. This suggests that forces originating through respiratory activity of protoplasm may be important in the secretion of dilute solutions; even possibly of those passing from the root cortex into the xylem. Evidence from experiments by KRAMER (**12**) and others, however, support the view that forces arising from metabolic activity of root cells that tend to move water into and through roots is negligible or quite secondary to forces created as a result of transpiration. It is the writer's opinion that exudation from decapitated plants (and exudation does not always occur) represents in large measure water movement brought about by the osmotic pressure of the tracheal sap when it is in excess of the sum of the osmotic pressure of the soil solution and capillary forces of the soil. In an intact plant even this force is of doubtful significance, except possibly during the recovery of turgidity, since the osmotic pressures in the foliar cells are greater than those of tracheal saps. The movement of water to leaves during transpiration (and after transpiration before turgidity has again been established) can be looked upon most logically as being the result of osmotic forces in excess of the inwardly directed forces exerted by cell walls. Plant roots can not be likened either to cylindrical tubes or to a porous medium such as soil. It is still probable, however, that the movement of water through roots obeys the law that has been found to hold in these other materials.

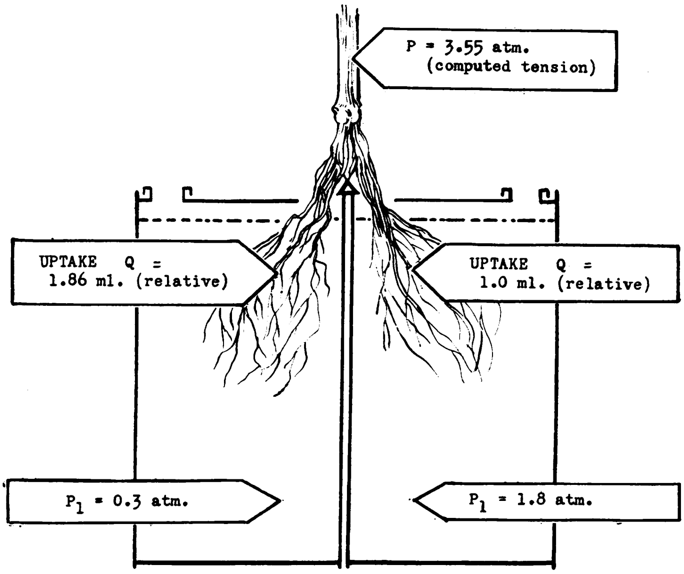

FIG. 5. Experiment 9. Water uptake, osmotic pressure, and tension relationships.

The flow of liquids through cylindrical tubes and through porous media has been found by POISEUILLE and DARCY, respectively, to be directly proportional to the difference in the hydraulic head of the liquid. For an approximate solution to the present problem, the most reasonable assumption we can make is that a similar relation holds for the transport of liquids through the conducting tissue of the plant. On the basis of this assumption and under present conditions where the gravity force is negligible compared with the pressure gradient force, one may write

$$Q = K (P - P_1)$$

where Q is the volume of flow in unit time, and $P - P_1$ is the difference in the pressure between the liquid in the conducting system and the liquid surrounding the roots. It is further assumed that osmotic and hydrostatic pressure differences are equally effective in producing the flow. The single value for the tension, P, of the water in the base of the shoot that satisfies both sets of water uptake and osmotic values is 3.55 atm. This value was obtained by substituting the two sets of experimental data in the above equation to obtain $1.86 = K (P - 0.3)$ and $1.0 = K (P - 1.8)$. Solving these equations simultaneously gives $P = 3.55$ atmospheres.

The foregoing value is necessarily an average one just as the water uptake values were the average of day and night uptake over the period of the experiment. With high transpiration rates the tension in the stem would become large, whereas at night as the plant regained full turgidity the tension would approach zero or become a positive hydrostatic pressure. From these relations it follows that as the tension increased the differences in the rate of uptake from the two solutions would narrow. On the foregoing basis, a tension of 10 atm. should produce an uptake of 1.15 ml. from the dilute solution for each 1 ml. uptake from the concentrated solution. As the tension fell to approach the value 1.8 atm., water would be withdrawn only from the dilute solution. Theoretically, at yet lower tensions there should be a movement of water through the roots from the dilute to the concentrated solution. It was not determined if this was the case, but BREAZEALE (**3**) has reported such flow through roots from moist soils into dry soils. The tension on the moisture of soils in the wilting range is about 16 atm., and according to recent experimental data by L. A. RICHARDS the soil moisture tension at the moisture equivalent is about 0.5 atmospheres. It is of some interest to note at this point that KEARNEY (**11**) found salts to have no effect on the wilting coefficient. This implies that if salts in the soil solution affect the tension between soil and plant there is some compensating effect within the plant.

It has been repeatedly found that the water requirements of plants on single solutions high in nutrient, chloride, or sulphate salts tend to be substantially lower than those of control plants. It has seemed more reasonable to attribute this to reduced transpiration rates resulting from salt effects within the leaves than to reductions in the osmotic differentials between the leaves and substrate.

ROOT DEVELOPMENT

The greater development of roots in the dilute than in the concentrated solutions (distilled water experiments as exceptions) might be attributed: (1), to conditions unfavorable to root growth in the concentrated solutions; (2), to conditions particularly favorable to root growth in the dilute solutions; or (3), to factors within the roots that caused more of the organic solutes translocated downward through the stem either to move into the dilute-solution roots or, having moved in, to be elaborated into tissue more rapidly. Either of these latter explanations would imply that the total growth of the root system as a whole had not been affected.

The fact that chloride, sulphate, and concentrated nutrient salts had similar effects would tend to discount the view that the concentrated solutions were especially unfavorable for root growth if all of the roots had been in one or the other kind of solution. It was noted in connection with experiment 1, where there was only a negligible root growth in the solution with 50 m.e. of chloride, that in other experiments with corn the roots of plants with all roots in 50 m.e. of chloride constituted a greater proportion of the weight of entire plants than was the case with plants growing with all roots in control solutions. In experiment 3 no appreciable difference was found in the moisture content of roots in the dilute and concentrated solutions.

In the absence of measurements on the distribution and concentrations of carbohydrates and salts in the two sets of roots of any experiment, discussion cannot be extended to the pertinent question of whether salt accumulations in the root tissues in the concentrated solutions tended to deflect the movement of organic materials from the shoots into the roots growing in the dilute solutions. A reason for a more rapid elaboration of synthesized products into cell structure in the roots containing less salt is not evident but the possibility that such was the case remains. A more rapid utilization of these materials by the dilute-solution roots would tend to establish more favorable translocation gradients to them.

As a final consideration some attention may be given to relations between the turgor pressures of roots and root growth. Cell growth by enlargement must be related to turgor pressure but one might question the extent to which the laying down of wall materials would be similarly influenced. ROBERTS (**16**) found the concentration of the cell sap of root hairs of radish growth in a series of 0.02 M to 0.65 M sucrose solutions to increase with the concentration of the external medium and maintain osmotic pressures 4 to 6 atm. above it. As further evidence of the adjustment of the plant to its substrate EATON (**6**) has presented the results of cryoscopic measurements on the expressed sap of a series of crop plants grown on saline solutions. The expressed sap of leaves of tomatoes, from the same seed stock as the present plants, when grown in out-of-doors sand cultures maintained osmotic differentials of 9.4, 8.9, 8.8, 9.5, 9.3, and 9.3 atm., respectively, above nutrient solutions as follows: control, plus 50 and 150 m.e. chloride, and plus 50, 150, and 250 m.e. sulphate. With this indication that the osmotic differentials between the root cells or leaves of a plant and its substrate are not greatly changed, within reasonable limits, by solutes added to the substrate, any conclusion with respect to disadvantages in water relations of the saline roots would have to be arrived at on some other basis. Otherwise, one might reason that since accumulation ratios are relatively high when plants are on dilute media and low when on concentrated media, that higher turgor pressures would exist in the dilute-solution roots than in the concentrated-solution roots. In other words, whatever the cause of the lesser root growth in the concentrated solutions may be, it is not reasonable to assign the cause to lack of turgor in the cells of the concentrated-solution roots.

AGRONOMIC ASPECTS

Prominent among the factors that tend to create differences in the concentration of the soil solution from point to point in irrigated soils there are especially to be mentioned: (1), variations in the permeability of proximately situated soil zones, even though of similar texture; and (2), the usually greater uptake by the plant of water than of salt, thereby increasing the concentration of the soil solution. The first-mentioned consideration gives rise to much lateral diversity since the less permeable zones are not leached as effectively as the permeable zones. The second consideration is largely responsible for the pronounced tendency for salt concentrations to increase with depth. The portion of a soil solution that is residual from a particular irrigation tends to be displaced downward in successive steps by successive irrigations and rains; thus the unused fraction ultimately lies deep in the root zone with a greatly reduced volume but still containing much of its initial salt.

Among other factors that influence both the average concentration of the soil solution as well as variations within the root zone, there are to be mentioned such considerations as the quality of the irrigation water, the extent to which water is used in excess of crop needs to promote leaching of the salts from the root zone, the amount of rainfall, methods of applying water to the land, and subsoil drainage conditions. Salt impregnated layers of clay as well as saline water tables are sometimes the source of salt brought into the upper root zone with rising moisture.

Both lateral and vertical diversity were illustrated in table I. As features pertinent to that example, it is to be noted that it had been the owner's policy to apply only sufficient irrigation water to maintain the trees from one irrigation to the next. Since the rainfall over a period of years prior to the collection of those samples had been subnormal there had been little recent leaching of the lower root zone. After two winters with leaching rains a much more uniform salt distribution was found. The irrigation water was of good quality containing but 0.29 m.e. of sulphate and 0.48 m.e. of chloride per liter. The soil samples were collected from beneath the irrigation furrows nearest the trees.

Summary

Corn and tomato plants were grown with their roots divided between two or more solutions of unequal concentration. They developed more

roots in the dilute than in the concentrated solutions and the water uptake from the former exceeded that from the latter. The foregoing was found irrespective of whether the differences in concentration were affected by the addition to the base nutrient of chloride, sulphate, or additional nutrient salts. Little difference in water uptake or in root growth resulted in solutions of similar osmotic pressure when one was high in chloride and the other in complete nutrient salts. These findings indicate that osmotic pressures, rather than specific ion effects, are primarily involved.

With an equal growth of the two halves a divided root system accomplished by alternating their positions each second day between dilute and concentrated nutrient solutions (0.3 and 1.8 atm.), 1.86 ml. of water was taken up from the dilute solution for each 1 ml. of water from the concentrated solution. A value of 3.55 atm. for the tension in the water of the stalk was found by calculation to satisfy these two sets of values on the basis of a first assumption that the observed water uptake by the two halves of this root system should be proportional to the difference in the osmotic pressure in the solutions and the tension in the water in the stem. This value is of course an average one and the data are discussed accordingly.

In an experiment parallel with the foregoing one, the two portions of the root system remained throughout in the solutions in which they were started. The new roots developed in the dilute solution weighed 1.6 times as much as those in concentrated solution and 76 per cent. of the total water taken up by the plant was from the dilute solution.

Roots divided between distilled water and concentrated nutrient made more growth in the latter. Almost twice as much water was withdrawn from the distilled water vessels during the first three days of the experiment as from the nutrient solution but this was later reversed.

The investigations were undertaken as a means of appraising the effects of the variability in the concentration of the soil solution often found within the root zone of plants growing on irrigated lands. When soils are permeable and extensively leached this variability may be slight but under other circumstances it may be great. An example is presented of the situation found in a permeable but lightly irrigated orchard soil wherein 15- to 60-fold variations in the concentrations of sulphate and chloride, respectively, were found within the root zone of single trees.

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