THE EXTENSION OF PLANT ROOTS INTO DRY SOIL[1]

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(WITH TWO FIGURES)

In the course of extensive fertilizer and irrigation experiments with guayule, there arose the questions of the ability of plant roots to extend themselves into dry soil and to absorb nutrients from such soil. These questions are of fundamental interest and of considerable practical importance, particularly in the case of the latter. The greatest concentration of available nutrient elements is usually in the topsoil, which is the first soil to become dry. If plants are not able to use water that is available to some other part of the root system for the absorption of nutrients by roots in "dry" soil, in some cases the elements added to the soil as fertilizers may be unavailable to the plant.

The literature records disagreement as to the ability of plant roots to extend into soil having moisture content below the permanent wilting percentage. HENDRICKSON and VEIHMEYER (**4**) concluded that the roots of sunflowers will not grow into soil which contains less moisture than is present at the permanent wilting percentage. SHANTZ (**8**) believed that the roots of some drought-resistant plants are able to penetrate dry soil, but that ordinary crop plants lack that ability. MAGISTAD and BREZEALE (**6**) and BREZEALE (**2**) made extensive studies of the moisture equilibrium between soil and plant and concluded that not only will roots elongate into dry soil, but the plant can absorb water through roots in moist soil, transport the water, and build up the moisture content of a dry soil to the wilting percentage.

An experiment was carried out in 1945 to investigate the penetration of roots into dry soil in atmospheres of varying degrees of relative humidity, and to study the uptake of nutrient elements from dry soil by roots of which a part were in moist soil. Corn was used as the experimental plant, in the belief that the findings would apply to other plants.

Experimental procedure and conditions

The photograph and schematic diagram of figure 1 show the arrangement of the component parts of the experimental apparatus. Sixteen pots of approximately 4-inch diameter and 8-inch height were prepared by brushing a mixture of equal parts of tar[2] (road oil) and paraffin (Parowax) on coarse cheese cloth, which was then shaped into cylinders with crimped-on bottoms. Examples of these pots are shown in figures 1 and 2. The walls and bottoms

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[1] Special Guayule Research Project, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, Salinas, California.

[2] The use of road oil as a component of this mixture was suggested by DR. A. C. HILDRETH.

were approximately $\frac{3}{16}$-inch thick. Before use the pots were filled with water and tested several days for leaks. All were water-tight. In order to further test the impermeability of the tar-paraffin mixture to water three air-dry Bouyoucos blocks (**1**) were coated with approximately $\frac{1}{4}$-inch of the material and immersed in water at room temperature for two weeks. Throughout the test the resistances of the blocks were above 250,000 ohms, indicating that no water penetrated the coating.

The pots were filled with a moist greenhouse potting soil and surrounded with approximately $1\frac{1}{2}$ inches of packed "dry" soil contained in wire mesh baskets lined with commodity cloth. One of the wire baskets with pot installed is shown in figure 1 (left). Approximately 4 kg. of air-dry Chualar loam, containing 0.4 per cent. moisture initially, was used with each pot. Its permanent wilting percentage and "field capacity" were approximately 4 and 12 per cent., respectively. With this soil was mixed approximately 0.5 kg. of dry quartz sand upon which a solution of radiophosphorus[3] had been dried. Four Bouyoucos blocks were spaced approximately equidistantly, in the air-dry soil, around the pot circumference, about midway between top and bottom and approximately $\frac{3}{8}$ inch from the pot wall. A similar block was placed centrally beneath the pot and another was installed inside it.

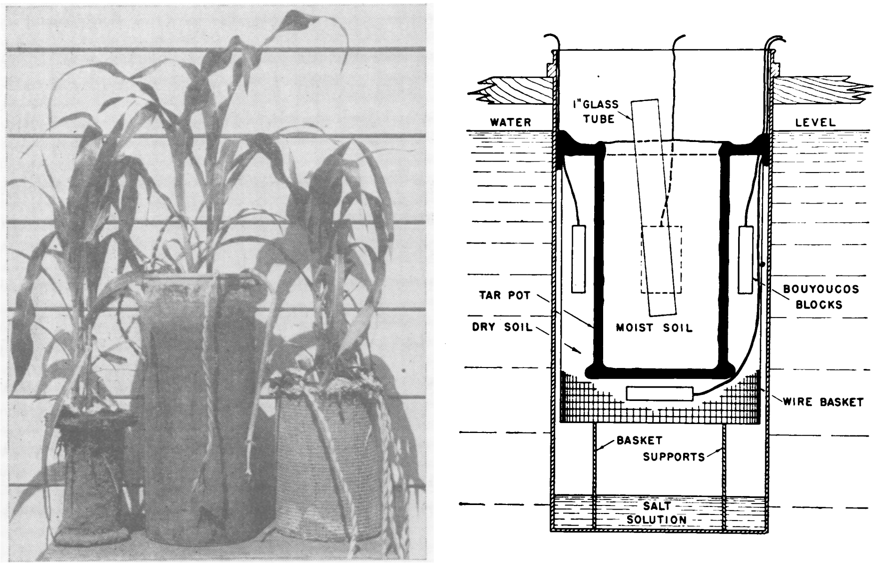

Fig. 1. Photograph and schematic diagram showing arrangement of component parts of experimental apparatus.

The screen baskets were supported 4 inches from the bottom of steel

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[3] The radiophosphorus (as sodium phosphate) was supplied to us through the kindness of Dr. Joseph G. Hamilton, Crocker Radiation Laboratory, University of California, Berkeley, California. The initial and final (after 30 days) quantities of radiophosphorus were approximately 17 and 3 microcuries per pot, respectively.

cans 18 inches tall. There was approximately ¼ inch of free air space between the walls of can and basket. The rims of the pots were sealed to the walls of the cans by means of collars of cloth to which the tar-paraffin mixture was liberally applied. These seals confined the "dry" soil to the atmosphere in the space between the tar pot and the steel can. Four different conditions of relative humidity, about the "dry" soil surrounding the tar pots, were obtained through the addition of salt solutions to the bottoms of the steel cans, below the wire baskets. Each condition was replicated four times. These conditions are listed in table I.

To avoid fluctuations in relative humidity due to changes in temperature, the 18-inch steel cans were immersed to a depth of 15 inches in a constant-temperature tank which has been described by CAMPBELL and PRESLEY (**3**). Throughout the test period the temperature was maintained at 84 ± 2° F. (except for one day, when a maximum of 88° F. was reached).

TABLE I

CONDITIONS OF RELATIVE HUMIDITY ABOUT THE "DRY" SOIL SURROUNDING THE TAR POTS

SERIES	POTS	ESTIMATED MAXIMUM RELATIVE HUMIDITY	ESTIMATED MINIMUM MOISTURE TENSION†	OBTAINED BY ADDING TO CAN
		PERCENTAGE	ATMOSPHERES	
A	3, 6, 12, 13	50	950	No solution
B	2, 5, 11, 16	82*	275	1 liter saturated NaCl (approx. 6 M)
C	1, 8, 10, 15	99*	15	1 liter 2.2 M NaCl
D	4, 7, 9, 14	100	0	1 liter water

* Calculated from Raoult's Law, $p = p_o N_1$.

† Calculated from the formula, tension in atmospheres $= \frac{RT}{0.018} \ln \frac{100}{\text{relative humidity}}$.

Three corn plants were grown in each pot. Water was added as required to the soil inside the pot to maintain a low moisture tension (resistance of Bouyoucos blocks around 500 ohms, or less). The resistances of the Bouyoucos blocks in the "dry" soil were determined at frequent intervals, usually two days, throughout the 30-day duration of the test.

The actual atmospheric conditions in the "dry" soil of the four series of pots were not determined. RUSSELL (**6**) indicates that the relative humidity of air-dry soil is about 50 per cent. The values of 82, 99, and 100 per cent. presented in table I are the highest values theoretically possible in equilibrium with the given solutions; it is very doubtful that values as these were actually reached during the test period. The estimated moisture tensions are the minimum values attainable in soil in equilibrium with the given maximum relative humidities.

Results and discussion

Twelve days after germination of the corn, pots 14 and 15 were removed for examination. Several roots had penetrated the pot walls and extended into the "dry" soil for about half an inch. The average moisture content of two separate samples of soil from the immediate vicinity of the roots was 1.04 per cent. for pot 14 and 0.80 per cent. for pot 15, as compared with an initial content of 0.4 per cent. The resistance of the Bouyoucos blocks was of the order of 35,000 ohms for pot 14 and 125,000 ohms for pot 15.

Pot 1 was examined after 24 days. Numerous roots had grown into the "dry" soil for one to two inches. The average moisture content of the "dry" soil about the roots was 1.12 per cent. and the average resistance of the Bouyoucos blocks was 31,000 ohms.

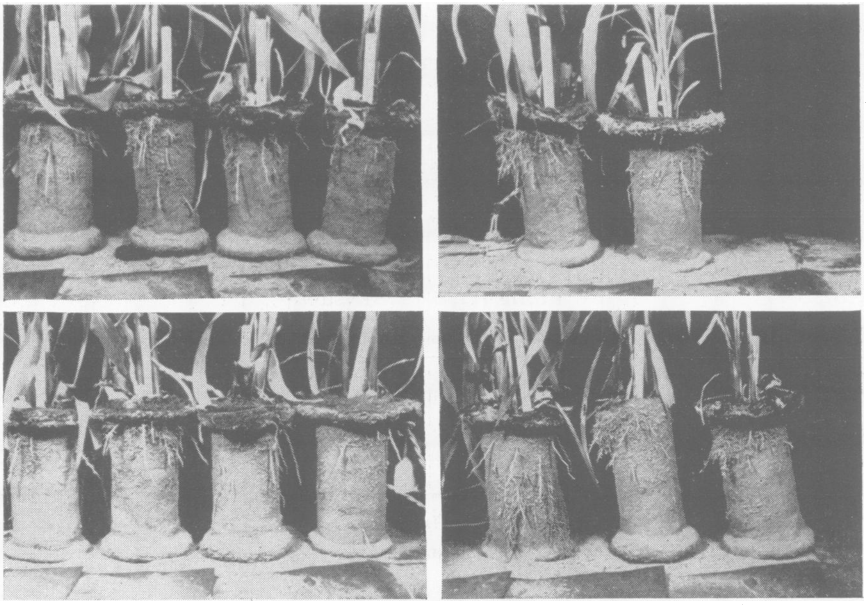

FIG. 2. Photographs showing corn roots that penetrated the walls of the tar pots and extended into "dry" soil at varying degrees of possible relative humidity, as follows: Upper left, Series A, approximately 50 per cent.; lower left, Series B, 82 per cent.; upper right, Series C, 99 per cent.; lower right, Series D, 100 per cent. Thirty days after germination.

After 30 days all the remaining 13 pots were removed and photographed. In every case, regardless of the conditions of relative humidity, many roots had extended into the "dry" soil, as is shown in figure 2. The surfaces of the roots were moist with exudate and in most cases had a thin sheath of adhering soil grains. Such a sheath was frequently observed by **MAGISTAD** and **BREZEALE** (**6**). That the soil about the roots was "dry" is evidenced by the fact that no brushing or other treatment was needed to free the roots of soil as they are shown in the photographs. Throughout the experimental period the resistances of the Bouyoucos blocks in the "dry" soil about these 13 pots were of the order of 250,000 ohms. **BOUYOUCOS** and **MICK** (**1**) state that the resistance at the permanent wilting percentage is around 100,000 ohms. Two samples (of 200–300 gm. each) of "dry" soil were taken from about each pot for moisture determination. The maximum, minimum, and mean percentage values, respectively, were as follows: Series A, 1.33, 0.70, and 1.00; Series B, 1.71, 1.11, and 1.29; Series C, 1.58, 1.16, and 1.27; and Series D, 1.25, 0.36, and 0.86.

All these moisture values are far below the permanent wilting percentage and all indicate a build-up of moisture in the "dry" soil. Since no water or solution was present in the cans of Series A, and the build-up of moisture in the soil of that series was practically as great as in either of the other series, the build-up in the "dry" soil must be attributed to the presence of roots rather than to absorption of water by the soil from the atmosphere surrounding it.

The tar-paraffin mixture was soft and plastic at the temperature of the experiment. The roots were continually growing and expanding, which tended to maintain extremely intimate contact between the root surface and the periphery of the hole in the pot wall at the point of penetration, preventing the seepage of water, alongside the roots, through the pot wall. Moreover, the surface forces of the "dry" soil, and its attraction for water, as the roots entered it, were much greater than the surface forces of the plant root. In such a case a film of water would not flow along a plant root surface through the "dry" soil, but would be "pulled" from the root surface and absorbed by the first dry soil with which it came in contact. For similar reasons water poured on a column of dry soil does not flow freely downward through any root channels or other openings that may exist, but is absorbed by the dry soil and moves downward as a moisture front. There is no reason to think that the build-up of moisture in the "dry" soil of this experiment was due to the flow of water along the root surface from the moist soil inside to the "dry" soil outside the pots. It must be attributed to the conductance of water through the tissues of the roots.

From the standpoint of the moisture stresses involved it is to be expected that plant roots will give up water and build up the moisture content of soil in which the moisture tension (or negative pressure) is higher than that of the root sap. The flow of water in plant roots is not polar. It is a familiar fact that water moves out of plant tissues and plasmolysis occurs if they are placed in solutions having greater osmotic pressures than the cell sap. MAGISTAD and BREZEALE (**6**) believed that there is an equilibrium between the plant and the soil, and with some plants at least, water moves either from the soil to the plant or from the plant to the soil, depending upon the nature of the moisture gradient. RUSSELL (**7**) states that the osmotic pressure of the root sap of most plants is of the order of 7 to 165 atmospheres as the soil moisture nears the wilting coefficient; for many plants it is around 15 to 20 atmospheres. The moisture tension in air-dry soil is around 1000 atmospheres (**7**); in soil at the permanent wilting percentage it is approximately 15 atmospheres. The fact that the soil moisture tension and the osmotic pressure of the root sap are both approximately 15 atmospheres in soil at the permanent wilting percentage may explain why plant root systems can build up the moisture content of dry soil to the wilting percentage but not above it, as BREZEALE (**2**) observed.

At the end of the experiment the aerial portion of the corn plants was tested with a Geiger counter for the presence of radiophosphorus. None was detected. This, however, cannot be taken as proof of the inability of roots to absorb nutrients from dry soil when moisture is available to them elsewhere. BREZEALE (**2**) showed that wheat seedlings were able to absorb potassium from soil initially at the permanent wilting percentage when water was available elsewhere in the root system. Had the corn been permitted to grow for a longer period, absorption of phosphate from the "dry" soil might have occurred. Relatively little of the "dry" soil was in contact with the roots. There is no way of estimating with any accuracy the amount of radiophosphorus in sufficiently close contact with the roots for absorption to take place under favorable circumstances. The presence of a probably ample supply of phosphorus in the moist greenhouse potting soil mixture in which the plants grow is a further factor which may have inhibited absorption of radiophosphorus from the dry soil. The results of this test are not conclusive as regards nutrient absorption from initially dry soil, but it is felt that a technique similar to the one employed can be used to answer the question. The authors attempted by another technique (**5**) to study the absorption of nutrients from soil in the wilting range.

Summary and conclusions

The extension of plant roots into dry soil was investigated. Corn was grown for 30 days in tar-paraffin pots filled with moist soil and surrounded by air-dry soil containing radiophosphorus. Bouyoucos blocks were installed in the "dry" soil for the periodic determination of its moisture condition. Variable conditions of relative humidity were maintained about the "dry" soil.

In all cases the corn roots penetrated the walls of the pot and extended into the "dry" soil. The moisture content of the "dry" soil increased, but values as high as the permanent wilting percentage were not obtained.

The results of the experiment indicate that the roots of corn are able to elongate into dry soil and to build up the moisture content of that soil. No evidence was obtained for the absorption of nutrients from dry soil by plants.

SPECIAL GUAYULE RESEARCH PROJECT
U. S. DEPARTMENT OF AGRICULTURE
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