Technical Bulletin No. 29 March 15, 1930

University of Arizona

College of Agriculture

Agricultural Experiment Station

MAINTENANCE OF MOISTURE-EQUILIBRIUM AND NUTRITION OF PLANTS AT AND BELOW THE WILTING PERCENTAGE

By

J. F. Breazeale

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*In cooperation with the New Mexico Agricultural Experiment Station and the United States Department of Agriculture, Bureau of Animal Industry.
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MAINTENANCE OF MOISTURE-EQUILIBRIUM AND NUTRITION OF PLANTS AT AND BELOW THE WILTING PERCENTAGE

By

J. F. Breazeale

INTRODUCTION

This bulletin is a report upon the progress of the work upon plant-soil relations at and below the wilting percentage, which was begun in this laboratory some time ago. In a recent bulletin(6), certain features of such relationship were discussed theoretically, and it is now the intention to support such discussion with experimental data. Many other important lines of investigation have been suggested during the course of work, and will be followed as time permits.

The ability of a plant to maintain water equilibrium within its tissues is well known. Water will move freely from fruit to leaves when the leaves are under stress, and it will move back again to the fruit, when this stress is relieved. Such phenomena in the above ground portion of the plant are often evident, and easily studied. The possibility of a plant maintaining equilibrium in the soil, has been suggested also(5), but for want of proper method of attack, and lack of technique, this has not been proved. The full role of the plant as a great equalizer of forces, has probably never been realized before.

In this work there were so many variables that it was often found to be almost impossible to grow pot cultures in duplicate, and have the results agree. Exact figures in such cases would represent individual cultures only, and are therefore superfluous, and often will be omitted. The author adopts as a criterion, the system of repeating each experiment over and over again, with as many variations and improvements in technique as possible, until he is satisfied that his conclusions are reasonably correct. It is assumed that, when such a system is followed in plant work, the opinion of an investigator should be of more value than his data, for his opinion is gained by experience and observation, details of which cannot be presented in full. When wide variations are unavoidable, even long averages have little meaning, and the selection of such data as may be presented under such conditions is, in itself, a matter of judgment. The data for single experiments will be given occasionally, either to illustrate the possible extent of the reaction, or to show the technique of the experiments, but it must be understood that absolute mathematical values are not intended. These facts should be borne in mind in any criticism of the data which will be presented in this paper.

During the past quarter of a century the author has handled millions of little plants in a technical way, and this experience has emphasized the difficulty of giving a mathematical expression to plant behavior. It is often impossible to put down the likes and dislikes of a plant in a tabulated form. It is equally as impossible to express health and vigor in terms of green or dry weight, transpiration, size of plant, or any other common criterion.

This bulletin presents the plant in the role of a great equalizer of forces. Whether these observations have a direct economic bearing upon crop production, is yet to be determined.

THE BEHAVIOR OF PLANTS AT THE WILTING PERCENTAGE

The behavior of plants at the wilting percentage is familiar, but not very well understood. It is a matter of fairly common knowledge among farmers, that the feeding roots do not necessarily die during periods of prolonged drought. The moisture in the root zone of the soil may be reduced to a point where none of it is available to the plant for transpiration purposes, and the plant may wilt temporarily, but, except in extreme cases, the root system remains alive although partially dormant. The roots will begin to grow and to function vigorously, when water is added again to the soil by rain or irrigation. It often happens in irrigation agriculture, especially with orchard crops, that the soil horizon which contains 50 percent or more of the roots, becomes "root dry" between irrigations during several months of the year. Orchard crops, however, are deep-rooted, most of them have tap roots which grow deep into the soil where moisture is usually available. These tap roots may prevent wilting, although the entire lateral root system, commonly known as the feeding roots, may be in a soil which has been reduced to the wilting percentage.

In dry-land agriculture, the crop is often made upon the water that comes as winter rains, and is stored in the soil or subsoil. In many cases, the available moisture of the surface soil is exhausted within a few weeks after the crop begins vigorous growth, and from then to maturity, the plants must depend upon the subsoil for water. The root zone, however, remains moist, that is, at near the wilting percentage, although there is some loss of water by direct evaporation from the surface.

It has been generally assumed that, when the surface soil is below the wilting percentage, and when there is no movement of water from the soil to the plant, there can be no absorption of plant food. If this is true, during at least a part of the growing season, there may be relatively long periods when the entire feeding root zone will be inactive as far as the nutrition of the plant is concerned. The plant must have nutriment in order to function, so if it cannot absorb plant food without absorbing water, the plant must draw both its water and its nutrient material from the subsoil by means of its deep, or tap, roots.

When there is a supply of available moisture in the soil, it is well known that a plant can absorb the water and leave the greater part of the dissolved salts in the soil. Furthermore, it is known that a plant can absorb the nutrient materials from such a soil, and leave most of the water behind, but, as far as can be learned, no actual proof has been obtained heretofore, which would indicate that a plant can absorb nutrients from a soil which is at, or below, the wilting percentage, or from a soil where practically all water movement has ceased.

As mentioned before, the soil in the root zone during a drought is reduced to the wilting percentage, or slightly lower, where it remains until the end of the drought. It does not become air-dry, although there is a certain amount of distillation taking place. Apparently some factor is operating which tends to maintain the moisture at approximately this percentage.

In the following discussion, two properties of the plant have been considered. First, its ability to remove nutrient ions from the soil after the movement of soil moisture practically has ceased, and second, its ability to draw water from one portion of the soil where there is a high percentage, and to return it to another portion where there is a low percentage, in order to maintain equilibrium.

GOOD CROPS WITH SURFACE SOIL AT THE WILTING PERCENTAGE

It has been demonstrated experimentally by Veihmeyer(9), that good crops of deciduous fruits may be produced in an orchard where the soil, to a depth of several feet, is kept at a little above the wilting percentage during a greater part of the growing season. In the system of citrus culture which has been used to advantage for many years upon the heavy soils of the San Joaquin Valley, California, the soil is allowed to dry down between irrigations until the trees show signs of distress. This system is being used with much success upon both citrus and deciduous fruits in Arizona. Under this system the surface soil is kept at approximately the wilting percentage for relatively long periods, and the beneficial effect upon trees, especially those which have been in poor condition previously, is very pronounced.

The author has observed, repeatedly, in the citrus orchards of southern California, where the basin system of irrigation is practiced, that the feeding roots do not die, and good crops are usually obtained, when water is withheld from trees for considerable lengths of time. In the basin system, a mulch of manure or other organic material, is put into the basin, and this treatment causes the main body of roots to develop very near the surface. When irrigation periods are far apart, 30 days for example, the supply of available water in the top layer of soil is soon exhausted, and the tree must depend upon its few deep roots for water until the next irrigation. The tree may wilt occasionally during the middle of the day, when transpiration is great, but wilting, apparently, is often a healthy condition. However, when the moisture in the root zone of the soil in the basin is reduced to the wilting percentage, or to a point slightly below the wilting coefficient as indicated by the centrifugal method of Briggs and McLane(1), or by the work of Briggs and Shantz(2), it remains fairly constant until more water is added.

FERTILITY OF SOIL AND SUBSOIL

The fertility of the soil is supposed to rest largely in the surface or cultivated zone. All fertilizers and manures are applied at the surface, and it is here that the feeding roots develop. It is well known that nutrient materials do not ordinarily penetrate farther than the lower edge of the plow layer. Nitrification takes places near the surface, and not in the subsoil, and especially under light irrigations, the tendency of nitrates is to move upward rather than downward. There is practically no downward movement of the phosphates and potash after they are applied to, and becomes fixed in the surface soil. In order to be fully effective all fertilizers must be cultivated into the soil. Certainly the crop-producing power of a soil is largely a function of the cultivated layer.

In humid regions, and in areas where there is a sharp distinction between the soil and subsoil, the subsoil is usually slightly toxic to plants. In the East, when the surface soil is removed in grading or terracing, and the planting is done upon the raw subsoil, little growth can be expected. The seeds germinate and the plants make a stunted growth, but feeding roots do not develop and usually no crop is produced. When it is necessary to plow deeper than usual in order to increase the depth of the plow layer, it is advisable to turn up only a thin section of the subsoil at each plowing, rather than to plow the full required depth at the first plowing. This is done in order to avoid mixing too much subsoil with the surface soil at one time. The toxic condition of the subsoil may be observed for several years after exposure, until organic matter is incorporated into the soil, or until cultivation and atmospheric agencies so change its nature that plants will grow in it. The same soil horizon that will support a normal tap root system will not support feeding roots.

During periods of drought, if the zone containing the feeding roots at or slightly below the wilting percentage, and if the assumption is that no absorption of plant food takes place under such conditions, we are forced to the conclusion that the plant is feeding in the subsoil which is known to be infertile and even slightly toxic.

THE WILTING PERCENTAGE OF THE SOIL

A silty-clay soil from near the San Xavier Mission, in the Santa Cruz Valley, Arizona, was used throughout this work. This will be referred to as the Mission soil. The soil was fertile already, but applications of potassium nitrate, in solution, were made at the rate of 200 to 500 parts per million. The soil was dried in an oven at 100° C., ground fine, and made up to the desired moisture content with tap water when needed.

This soil has a moisture equivalent of about 35, as measured by the centrifugal method. This figure, when divided by the factor 1.84, should give a wilting coefficient of about 19.

The accuracy of this method is not now under consideration. It may be stated, however, that, while wheat plants usually wilt permanently at this percentage, under certain conditions they may be made to reduce the soil to about 16 percent. The term "wilting percentage," or "wilting coefficient," are often misleading. The wilting zone in this soil, for example, ranges from 16 to 19 percent, depending upon the plant, upon root distribution, length of roots, rate of transpiration, and whether or not some water is available to a portion of the root system.

If the centrifugal method of determining the wilting percentage is not correct, the writer knows of no way of checking its accuracy definitely. There is no direct method of determining the wilting percentage by the use of plants, which does not involve several errors. The wilting percentage is largely a function of the layer of soil which lies in direct contact with the absorbing zone of the roots, and no way of separating this layer of soil from the root, and determining its moisture content accurately, has yet been devised. It must be remembered, also, that the absorbing zone does not include the entire length of the root, and that the greater part of the root is often coated with an impermeable covering which prevents desiccation. It is true also that the suction force of the root cells of certain plants is increased with the decrease in moisture, however, this increase does not greatly affect the amount of water which is available. The ability to absorb water is not even necessarily uniform in the root area that is known to be the absorbing zone.

If a plant is drawing water at a definite rate from a soil layer, this water will be replaced by the water in the adjoining soil. In a saturated soil this rate of film water movement is fairly rapid, but, as the moisture is decreased the rate decreases rapidly, until at the wilting percentage, when the film is only about 100 molecules thick, the movement is very slow. The percentage of moisture within the thin layer of soil in contact with the root tips, may or may not be the same as that in the soil even a short distance away. If plants are grown in a certain volume of soil until they wilt permanently, and if all the soil is then used in the moisture determination, the results obtained will represent the average percentage of moisture, and not the percentage in the soil which has been in contact with the root tip or root hairs. As the amount of soil in contact with the root may be relatively small in comparison with all of the soil in the culture, this error may be very large.

Another error may be involved in the root volume, or in the distribution of the root system. A certain number of plants with roots well distributed in the soil, should absorb more water from a given weight of soil, than the same number of plants with the same root system confined into a narrow range. Another error may be involved in the length of the root. It has been the observation of the writer that the short roots, or those which lie in the upper layer of the soil, are probably more effective in the absorption of water than are the long roots which grow deep into the soil. In the age of adaptation, the stimuli would have been for the development of just such a difference in character. This will be discussed later, in more detail.

The rate of transpiration of the growing tissues above ground should involve another error. A plant growing in an atmosphere with a high relative humidity, should be able to draw more moisture from a soil before wilting, than one growing in an atmosphere with a low relative humidity. A plant can transpire no more water than that which is delivered to its roots by the soil. If the demands of transpiration are greater than the supply of moisture, which in turn, is dependent upon the rate of movement of film water in the soil, the plant must wilt. If the rate of movement is slow, the wilting of a plant should take place much sooner during high than during low periods of transpiration.

Probably the greatest error in a direct determination of the wilting percentage rests in the ability of certain plants to accommodate themselves to low percentages of soil moisture. When the rate of movement in the soil is slow, succulent plants like lettuce, cannot wait for the moisture to be delivered to their roots, so they wilt and die. During its age of adaptation, lettuce was probably not subjected to arid conditions, and it has not, therefore, developed drought-resisting adaptations. Wheat, on the other hand, originated in the semi-arid region, and therefore it can tide over moderately long periods of drought, and can accommodate itself to the slow movement of water in the soil. Cactus, as an extreme type of plant, is accustomed to desert conditions, and it can wait for its water for long periods of time. If the vitality of lettuce could be maintained under conditions of stress as long as that of cactus, each plant would probably show the same wilting percentage. Under ordinary conditions the wilting percentage, if measured by lettuce, should not represent complete equilibrium with respect to moisture in the soil. If wheat is used instead of lettuce, soil equilibrium should be approached more closely, while with cactus the soil might have ample time to adjust itself, and to come to almost complete equilibrium. In the consideration of plant-soil relationship at the wilting percentage, the above mentioned phenomena are of much importance.

It is believed that similar plant root cells which absorb water, manifest approximately equivalent suction forces, regardless of the plant to which these cells belong. All plants have felt many of the same stimuli, and with reference to the absorption of water from the soil, they have probably all developed similar adaptations. However, these characters are only approximately the same. While the suction force of a plant may be assumed to average about 5 to 8 atmospheres, this is by no means a mathematical constant. If all plant characters were constant, the plant would not possess the power of accommodation or adaptation. The plant must have a range of activity. There is a range in the suction force of the plant from about four to about fourteen atmospheres, and this range is probably different with each species, and probably different with individuals of the same species. This range may seem wide, but when all factors are considered it is evidently narrow.

In this bulletin, the wilting percentage is assumed to be the state of equilibrium which exists between the suction force of the plant and the adhesive forces of the soil, a condition which probably cannot be measured with any great degree of accuracy. When used in connection with soil conditions the term "wilting percentage" is intended to imply the "wilting range," rather than any one definite percentage.

It really makes little difference whether the methods as designed by Briggs and Shantz(2), for obtaining the wilting coefficient represents the true wilting percentage of any soil. It, at least, gives a definite standard of comparison. As in the case with the metric system, the meter is a valuable and definite standard, regardless of the fact that it does not represent one ten-millionth part of the earth's meridian quadrant, as it was supposed to do when it was adopted.

ABSORPTION OF WATER, AN ADJUSTMENT OF FORCES

The absorption of soil moisture by plants may be looked upon as an adjustment of forces. In figure 1 is shown, graphically, a plant root (a) in equilibrium with a layer of soil particles (b). Under such conditions the film water (c) is about 100 molecules thick, and is continuous from the soil to the root surface. The suction force of the root is assumed to be a constant, and equivalent to 5 to 8 atmospheres. At equilibrium, the adhesive force of the soil should balance the suction force of the plant, and no movement of water from plant to soil should be possible. If water is added to the soil, the thickness of the film will be increased, the adhesive force of the soil particles will be decreased, and equilibrium will be upset. As the plant cells have actual moisture contact with the film upon the soil particles, water will move from the soil to the plant until equilibrium is restored.

On the other hand, if water is removed from the soil by direct distillation caused by the heat of the sun, the soil film will be decreased in

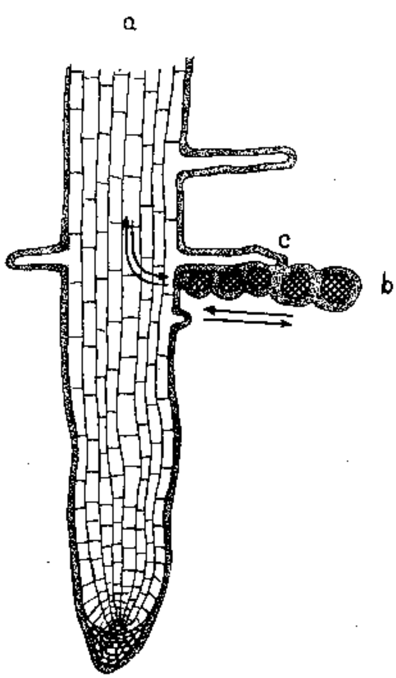


Fig. 1.—A plant root in equilibrium with soil particles.

thickness, the adhesive force will be increased greatly, so instead of a force of from 5 to 8 atmospheres, the pull of the soil may amount to over 25,000 atmospheres. Water must move now from the plant to the soil until equilibrium is established, or until the plant dies. In the figure the double arrows indicate the direction of water movement.

AVAILABLE MOISTURE

At its saturation point, the attractive force of the soil amounts to gravity only, or 0.001 atmosphere, at its optimum moisture content the force is 1000 gravity, or one atmosphere, and at the wilting percentage it is 5 to 8 atmospheres. Available moisture in the soil, therefore, is that water which is held by the soil with a force of less than 5 to 8 atmospheres.

It has been a matter of much discussion as to whether all of the moisture above the wilting percentage is equally available to plants. It is the opinion of the public in general that plants grow best when the moisture content of the soil is made to fluctuate up and down, but always maintained at near the optimum. As a matter of course, every one recognizes the difficulty of maintaining a very low percentage of available moisture in the soil, however, this difficulty may be purely mechanical or physical.

It has been observed by Veihmeyer (9), that plants can absorb moisture from soils which are only slightly above the wilting percentage, quite as readily as they can from soils at the optimum moisture content. The Mission soil, for example, with a moisture equivalent of 35, has a wilting coefficient of about 19. According to the views of Veihmeyer, if this soil, in the field, had a moisture content of 22 percent, and if this moisture supply could be maintained constant, the water above the wilting coefficient, or 3 percent, would be as available for transpiration purposes as moisture would be in the same soil at 35 percent. There appears to be no direct ratio between the percentage of moisture in the soil and its availability for plants.

When this phenomenon is first presented it seems unreasonable, but upon due consideration it is just what should be expected. The absorption of water from a soil is a function of the suction force of the plant. If the suction force expressed in atmospheres, is plotted against the percentage of soil moisture, a curve (Fig. 2) is obtained. It will be seen that the curve is very flat from a point a little above the wilting coefficient, or about 19 percent to the position of the moisture equivalent, or 35 percent. It would therefore require very little more effort on the part of the plant to remove the film water from this soil at 22 percent than from the soil at its optimum moisture content. The difference

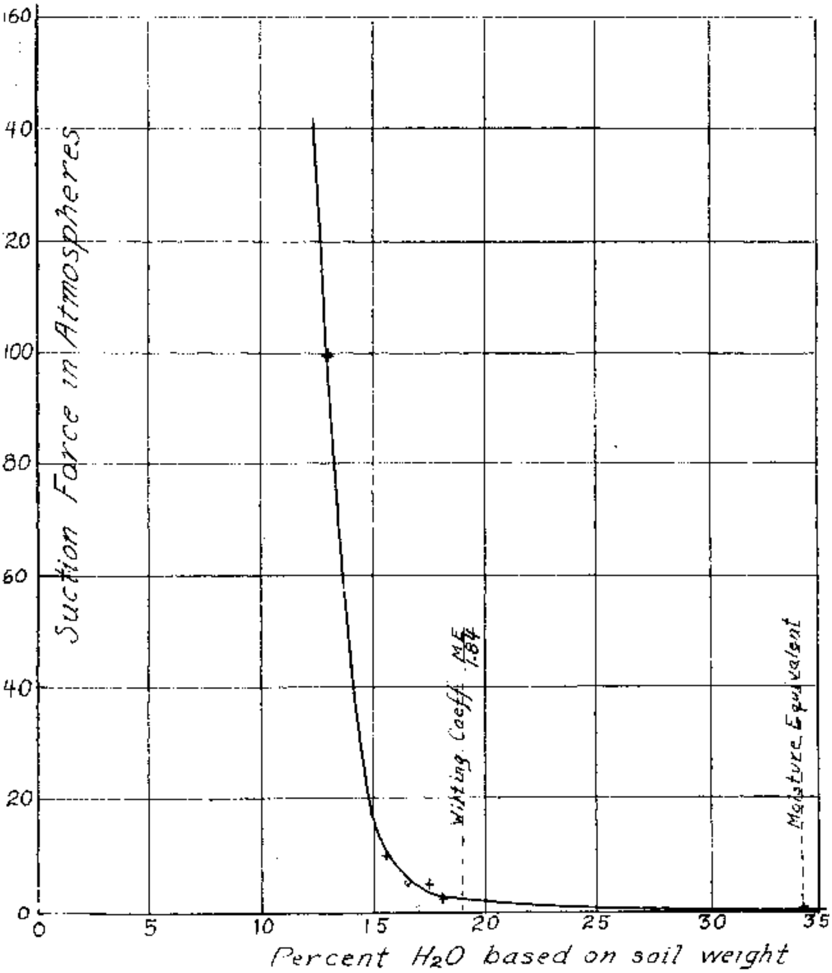


Fig. 2.—Graph showing force with which water is held in a silty-clay loam at varying moisture contents.

in suction force thus required would amount to only one or two atmospheres, and this difference might be adjusted easily by the "suction range" of the plant.

Furthermore, at the optimum moisture content, the outer layer of molecules of the moisture film is held to the soil by an adhesive force of about one atmosphere, while the layer 100 molecules away from the soil particle in the same film is held by a force of 5 to 8 atmospheres. If a root tip with a suction force of about 7 atmospheres touches this film, the outer portion of the film will be absorbed and equilibrium will be reached. The final equilibrium will represent an adhesive force of about 7 atmospheres. The root will absorb all of the molecules except those lying within a distance of the thickness of a layer of 100 moluecules from the particle, so, in order to get all of the available water from a soil at optimum, the plant must exert a force, beginning with one atmosphere with the outer layer of molecules, and ending with seven atmospheres with the inner layer, or an average of 3 atmospheres.

When a plant is growing in a soil at the optimum moisture content, the absorbing root tips are actually in film contact with a relatively small amount of soil, and are drawing water from a relatively few soil films. Eliminating the fact that plant roots elongate, we can assume that water must move through the soil to supply that which is absorbed by the plant. Even in a soil at optimum, this movement is too slow to maintain the soil film which is in contact with the root tip at its maximum thickness. It is generally assumed that, when a plant is drawing water from a soil at the moisture equivalent, it is operating against an adhesive force of only one atmosphere. This is far from being true. In all probability, moisture films in such a soil, in contact with an active plant root, are very thin, relatively, and the soil area in contact with the root is probably seldom very much above the wilting percentage.

A plant may be compared to a suction pump, the first stroke of which may deliver water from a well, from a 10-foot level. If, however, the lateral movement of water in the soil is slow, the draw-down in the well may be so great that, after a few strokes, the pump will have to draw water continuously from a 50-foot level.

These facts are applicable to the observation of Veihmeyer, which has just been referred to. In the amount of resistance to be overcome by the plant, it probably makes little difference whether the soil is only slightly above, or very much above the wilting percentage. The plant is most concerned with the movement of water within the soil. These conditions, however, will be modified, if the plant root is elongating continuously.

EXPERIMENTS WITH SOIL AND SOLUTION CULTURES

In semi-arid agriculture, and during periods of stress in all agriculture, water is often the limiting factor. If the entire root system of a plant is confined to a soil which is maintained at or below the wilting percentage, the plant will die, no matter how fertile the soil may be. Even during periods of prolonged drought, there is usually a supply of water in the subsoil, although a scarcity may exist in the root zone. This represents unstable equilibrium in the soil, and apparently the plant has met this situation by developing the property of absorbing water from one zone where it is plentiful, and returning it to the soil where most needed. As far as water alone is concerned, this is only a temporary expedient, which enables the plant to tide over periods of drought. Whether this water, which is returned to the soil, can dissolve and render plant foods available, will be considered also.

As the plant is concerned with a very thin soil layer adjacent to the absorbing root tip, as the amount of water exuded by the plant must be small and as the amount of plant food under consideration must be small, also, the difficulties in the way of the investigator are evident.

THE CULTURE POTS

Culture pots of earthenware, porcelain, glass and paraffined cardboard, as shown in figures 3, 4, 5, 6, were used as the occasion demanded. The earthenware and cardboard pots were always dipped in hot paraffin in order to render them impermeable to water.

In figure 3 is shown a porcelain pot of a type which was frequently used. These pots were electric light mantles originally, and may be obtained in all shapes and sizes. When the openings in the bottoms of such vessels are too large they may be stopped with a cork, and a hole the proper size cut through the cork.

In figure 4 is shown a glass percolating tube which was converted into a culture pot. Glass or porcelain pots are to be preferred, for the reason that there is no loss of soil moisture, due to evaporation through the walls, as in the case with unglazed earthenware.

In figure 5 are shown two ordinary shallow, 5-inch, unglazed, earthenware pots, as they were used in this study. There was usually some loss by evaporation through the walls of such pots, unless they were thoroughly paraffined both inside and outside.

In figure 6 are shown two small cardboard ice cream cartons which, when paraffined, proved very useful. As these held only a small amount of soil, they could be weighed fairly accurately, and the gain or loss of moisture determined directly.

GROWING THE SEEDLINGS

In these experiments only hardy seedlings could be used to advantage. Many attempts were made to use corn, popcorn, milo, and other plants, but with unsatisfactory results. Many plants have brittle roots, and these break or crack under the rough treatment to which they must be subjected. These broken roots are apt to "bleed" and thus add water to the soil. Wheat and barley seedlings were the most satisfactory, and unless otherwise stated wheat was used in all the work.

Wheat seeds were germinated upon perforated aluminum discs, which were floated in large pans of water, and when the plumules were about 2 centimeters long, the seedlings were withdrawn in sets of 25, and transferred to tall culture bottles of about 1 liter capacity. In most of the work, the plants were allowed to grow in these bottles, in tap water, for about 12 days before they were transferred to soil cultures, and placed under observation.

As it was necessary in this work to have plants with long and vigorous root systems, from 5 to 10 parts per million of pyrogallol was added to each of the culture pans. The use of pyrogallol was first suggested to the writer, many years ago, by Professor Milton Whitney of the Bureau of Soils, United States Department of Agriculture, who thought that probably this reagent might act as an oxidizing agent upon the toxic compounds of the soil. The writer found that, in concentrations just mentioned, it stimulated root development to a wonderful degree. This phenomenon has not yet been explained satisfactorily, but long roots. with relatively few laterals are certainly produced in such solutions. As will be seen later, it would have been very difficult to have carried on this work, had it not been for the use of pyrogallol.

When a satisfactory top growth had been made, and when the roots had reached the length of about 20 centimeters, the plants were removed from the culture bottles, and prepared for observation. The excess water on the roots was removed by pressing the roots lightly between blotting papers, and a thorough contact with the soil was then made, by rolling them about in the prepared soil, until they were dovered entirely with soil. The plants were then ready for use.

TECHNIQUE OF THE EXPERIMENTS

The plants were placed in the culture pots, with the lower parts of their root system extending through the hole in the bottom, and into tall beakers or graduated cylinders of water, or into moist soil when so desired. (Fig. 3.)

The hole around the roots was plugged with vaseline which had been worked up with a small amount of cotton (b). Soil of a known moisture content was packed into the pot around the roots, and a mixture of paraffin and beeswax, of low melting point, was poured over the top. (a). A control pot was prepared at the same time with all of the plant roots in the soil.

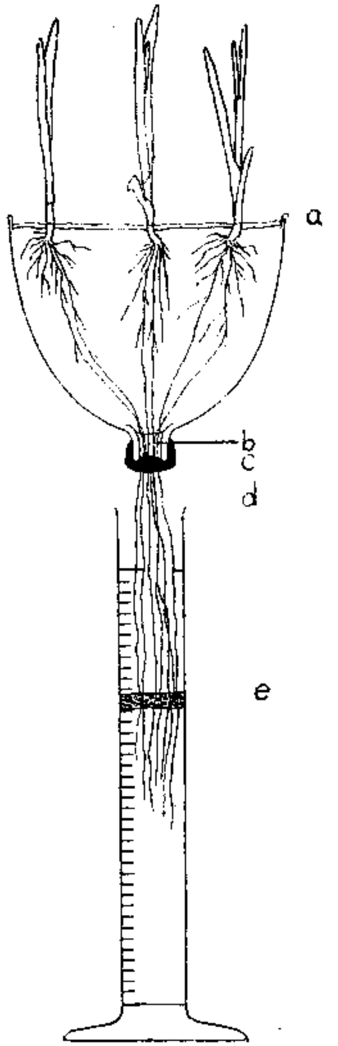


Fig. 3.—A porcelain culture pot over a cylinder of water.

An important source of error in such a measurement of the movement of water lies in the capillary rise upon the surface of the roots, or the so-called "wick action," and many changes in technique were found necessary in order to obviate this difficulty. It is very difficult to distinguish between the water which has risen by capillarity upon the surface of the roots, and is absorbed by the soil, from that which comes up through the cells in the interior, and is distributed. In most of the work, a little dry plaster of Paris was first rubbed in between, and around the roots where they emerged from the pot. As is well known, when plaster of Paris—$CaSO_4 + \frac{1}{2}H_2O$—comes in contact with a limited amount of water, it absorbs the water with an enormous force, and "sets," that is it becomes a mixture of $CaSO_4$ and $CaSO_4 + 2H_2O$. It

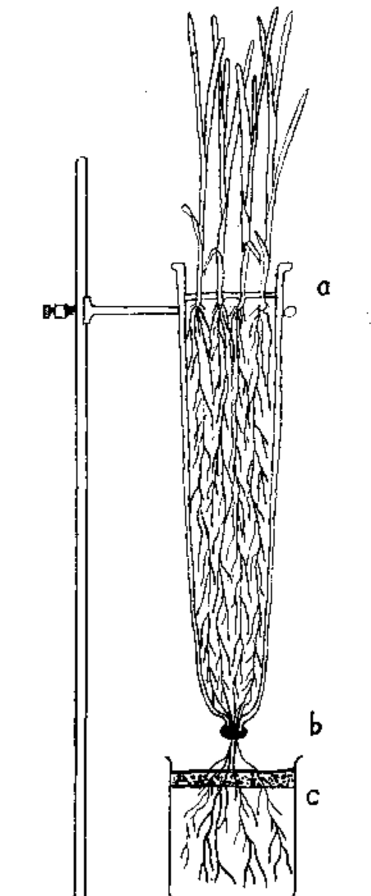


Fig. 4.—A percolating tube converted into a culture pot.

was assumed that, by rubbing dry plaster of Paris against the root, the setting would draw away the moisture, and break the capillary film.

After a few minutes, in order to allow for the setting, a quantity of plaster of Paris was worked up with water, and a large mold was pressed around, and between the roots. (Fig. 3-c.) When the plaster was set firmly, it was covered with a layer of vaseline as far down as the surface of the water. (Fig. 3-d.) A pure, heavy, mineral oil, such as is commonly used in medicine, was then poured over the surface of the water to a depth of about 1 cm., (Fig. 3-e), and the cultures were then ready for observation. The pots could be removed and weighed whenever necessary, and any nutrient could be added to the water in the reservoir below. No difficulty was experienced in the growth of seedlings due to this treatment. The roots elongated beneath the oil seal, and apparently did not need aeration during the periods of observation. The surface of all roots was covered with a film of water, so the raising or lowering the roots through the oil, probably did not disturb this film.

The distance between the soil in the pot and the free water surface, (b) to (e), was determined by the length of the roots which were available. It amounted to as much as 17 centimeters. In order for water to rise by capillarity over the root surfaces and reach the soil, it would have had to pass through 1 cm. of heavy oil, through about 13 cm. of vaseline and 3 cm. of plaster of Paris. If any such capillary movement did take place under these conditions, it was certainly reduced to a minimum.

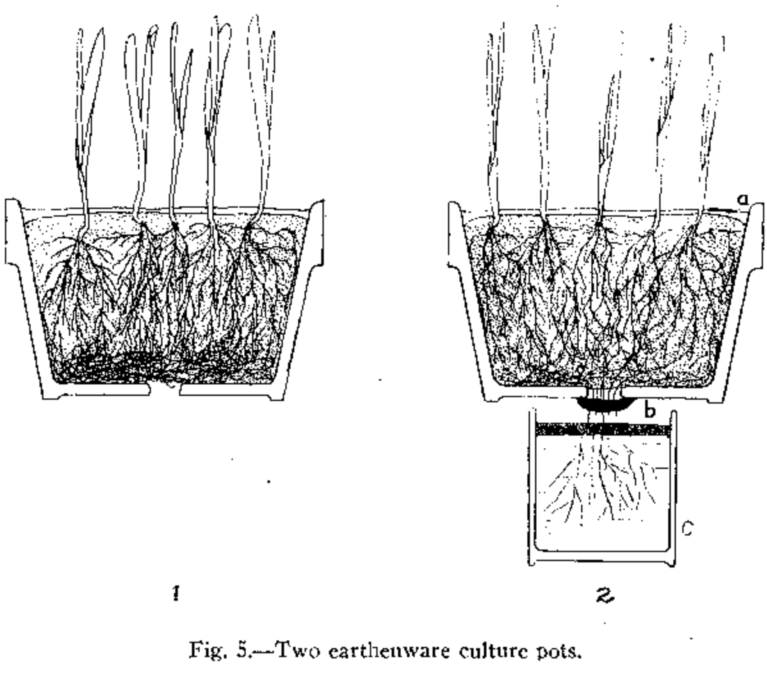


Fig. 5.—Two earthenware culture pots.

THE BUILD-UP OF SOIL MOISTURE

When air-dried soils, or soils with a moisture content below the wilting percentage, were placed in these pots, and in contact with plants

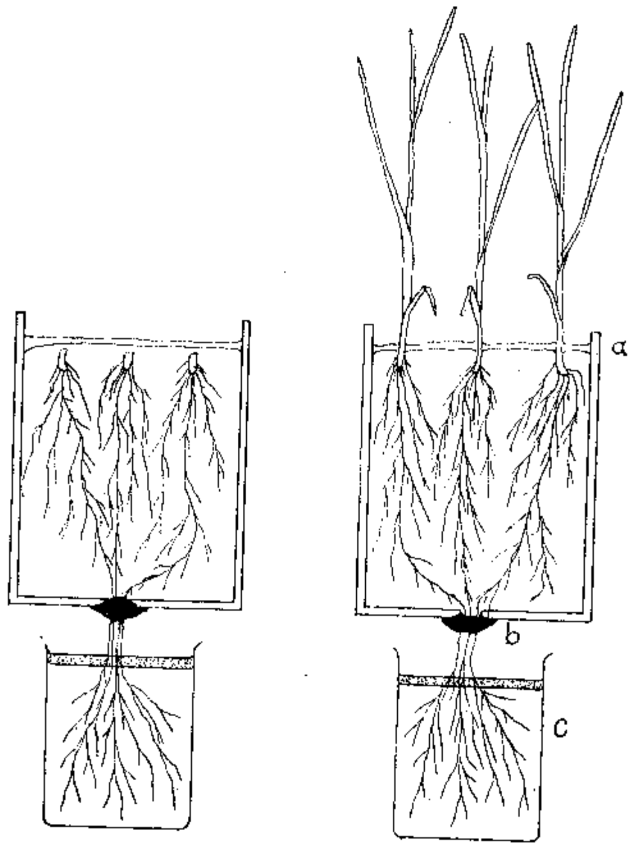


Fig. 6.—Two ice cream cartons converted into culture pots.

whose roots had access to free water, an increase in the moisture of the soil in the pots was nearly always noticed. The build-up of moisture usually was rapid at first, then it lessened gradually, until the wilting percentage was reached, when the build-up usually stopped. The rapidity of the build-up depended largely upon the distance from the soil to the free water surface, the original moisture content of the soil, the effectiveness of the contact between the roots and soil, the number of plants in the culture, and possibly upon other factors.

A build-up above the wilting percentage was obtained occasionally by covering the plants with bell jars. Unless the plants were so covered, transpiration from the leaves prevented the moisture in the soil from being built up above the wilting percentage, for above this point the moisture would be available, that is, the pull of the plant would be greater than the pull of the soil, and the water would go to the plant and be used in transpiration.

The total amount of water which was used for transpiration purposes exceeded greatly the amount used in building up the moisture content of the soil. The total amount of water used was obtained from the readings upon the graduated cylinder, while the build-up of soil moisture was determined by removing the pots occasionally and weighing them, or by a determination of the moisture in the soil before and after the experiment. The difference between the total amount of water used, and the amount used in the build-up represented the loss by transpiration. The increase or loss in weight of the plants involves a small error, which may be determined and allowed for when necessary.

It must be remembered that actual values vary with conditions, but data for one experiment will be given, in order to illustrate more fully the methods used. A set of 25 10-day-old wheat seedlings was placed in a paraffined carton, with 460 grams of air-dried soil, of a moisture content of 5.8 percent, or an equivalent of 435 grams of oven-dried soil. The roots of the plants were carried through a hole in the bottom of the carton, and into a reservoir of water, as shown in figure 7, No. 4. The plants were sealed in securely, as has been described, and one centimeter of heavy oil was poured over the top of the water. The distance from the soil to the free water surface was 13 or more centimeters. The cultures were kept under observation for 22 days, and the data are shown in Table I.

TABLE I.—TRANSPIRATION OF PLANTS AND BUILD-UP OF MOISTURE IN AN AIR-DRY SOIL.

Total amount water absorbed from cylinder	213.0 gms.
Increase in weight of pot	17.0 gms.
Transpiration	196.0 gms.
Total moisture in soil at end of experiment	40.0 gms.
Total moisture in soil at beginning of experiment	25.0 gms.
Build-up of moisture in soil	15.0 gms.

The build-up in this experiment was relatively slow, however, 15 grams of water were absorbed from the cylinder, transported through the roots by the plants and added to the soil. It will be noted that over ten times as much water was used for transpiration purposes, as was used in the build-up of moisture in the soil.

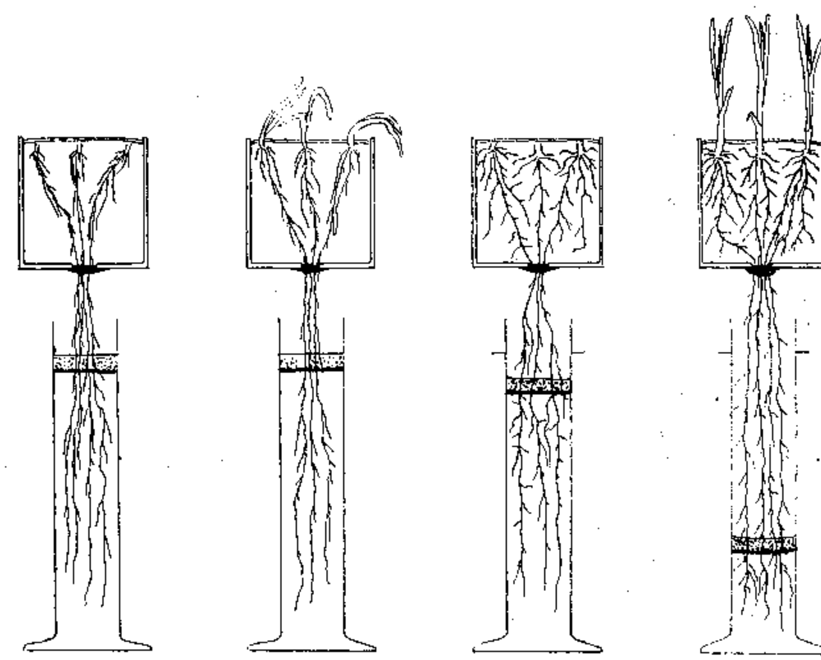
CAPILLARY OR WICK ACTION

As mentioned before, the greatest probable error lay in the capillary rise of moisture over the outer surface of the roots. Whether this was overcome effectively by the methods which have been described, is shown in the following experiment:

Four sets of seedlings were removed from the water culture bottles and placed under observation as shown in figure 7.

No. 1. The tops were cut off, and the roots dried for several hours at 100°C. The dry roots were then placed in a pot of air-dried soil, with the lower part of the roots in water. The top of the pot was sealed with warm paraffin-vaseline mixture, and vaseline and plaster of Paris were used on the roots in the way which has been described already.

No. 2. The tops were not removed, but the entire plant was dried at 100°C. and planted the same as No. 1.



1 2 3 4

Fig. 7.—Four ice cream cartons with cylinder reservoirs.

No. 3. The healthy growing plants were placed in the soil with the lower parts of their roots in water. The tops were then cut off, and the paraffin-beeswax seal poured over the soil as shown in the figure.

No. 4. Healthy growing plants were placed in the cultures in the usual way.

After standing 48 hours the approximate loss of water from the graduate cylinders is graphically shown in the figure. Neither the dead roots (1), nor the dead plants (2), showed any tendency to withdraw the moisture from the cylinders. If there had been a tendency for the soil to build up its moisture content in these two cultures, the build-up could safely have been attributed to capillarity, or to the wick action of the roots. Apparently the treatment with vaseline, plaster of Paris, and heavy oil had checked such action effectively.

There was a slight upward movement, and build-up in the case of the live roots in No. 3, but this upward movement stopped after a day or two. Although there were no tops on these plants, and, therefore, no transpiration, there was a distinct upward movement of water. The roots of these plants did not die for several days after the tops were cut off, and, while alive, they probably absorbed some moisture, and transferred it to the dry soil.

The plants in No. 4 continued to absorb water, and to build up the soil until it reached the approximate wilting percentage.

On several occasions, after healthy plants, like those in culture 4, figure 7, had made a substantial build-up, they were killed by removing their roots from water, and allowing them to dry in the sun, without disturbing the plaster of Paris and vaseline seals. When the dead plants were placed again under observation, no build-up of soil moisture was obtained. Data upon one experiment of this nature will be given.

Twenty-five healthy seedlings were placed in a paraffined ice cream carton with 400 grams of air-dried soil, with a moisture content of 5.4 percent. The culture was then sealed with paraffin-beeswax, plaster of Paris, etc., as has been described before. It was kept under observation for 20 days. A hole was then cut in the paraffin seal on the top, all the soil removed, and a moisture determination made. A build-up from 5.4 percent to 16.6 percent was observed.

The tops were then cut off the plants, and the roots dried down thoroughly, without disturbing the plaster of Paris seal. Fresh, air-dried soil then packed into the pot and sealed over with warm paraffin-beeswax. No further build-up of soil moisture was obtained.

Evidently it is possible to eliminate capillary, or wick action, of the roots almost completely by the use of vaseline, plaster of Paris, and heavy oil seals.

In figure 8 is shown an illustration of a culture, with the soil arranged in two layers, and separated by a thin disc of paraffin. As has been stated before this soil has a wilting coefficient of 19, and the build-up, under these conditions, cannot exceed this percentage.

In cultures of this type the lower soil layer, (c), was made up to about the wilting percentage, or 19 percent, while the top layer, (a), was put in relatively dry, 5 percent. The lower layer could not give up any moisture to the plant, nor could it absorb any water from the roots, but the water which went to build up the top layer had to pass through this lower layer.

The data of one experiment of this kind, in which 25 plants were kept under observation for 5 days, are given in Table II.

It was assumed that the sandwich of soil at the wilting percentage, between the free water and the dry soil, would have a tendency to stop all water which might rise by capillarity, or wick action, upon the

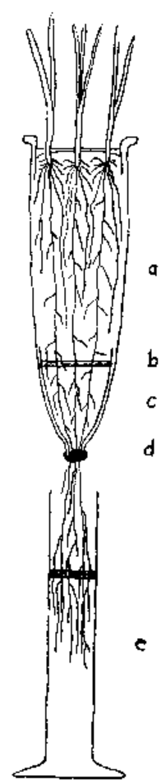


Fig. 8.—Illustration showing how water may pass through a moist soil and build up the moisture content of a dry soil.

surface of the roots. Evidently some water within the plant roots passed through the lower layer, and was absorbed by the upper layer.

TABLE II.—MOISTURE BUILD-UP THROUGH SOIL AT THE WILTING PERCENTAGE.

	Percent moisture		Build-up	Transpiration
	Beginning	End		
Soil in top layer — 500 gms.	5.0	10.0	25.0 gms.	44.0 gms.
Soil bottom layer	18.0	.....	.....	.....

Even if the wick action of the roots was an important factor in these experiments, and could not be eliminated completely, it must be remembered that such action may also take place under field conditions, and that this may affect the distribution of moisture. In the application of the results, it really makes little difference if a small amount of moisture moves by capillarity, rather than by cellular movement.

TRANSFER OF MOISTURE FROM A MOIST TO A DRY SOIL

In most of the experiments with pot cultures which have been described, a part of the root system was in contact with free water, and the transfer of moisture, therefore, took place from free water to a dry soil. This condition is analogous to a plant growing in the field, with a water table in reach of its tap root, but with its feeding roots in "root-dry" soil. However, as before mentioned, water moves readily from one part of a plant to another in order to equalize moisture deficiencies in any particular part. The writer has repeatedly built up the moisture content of a dry soil by allowing the leaves of wheat plants to come in contact with the soil.

If this is done under a bell jar, and in a saturated atmosphere, the water which is transpired by the plants, will be absorbed by the soil until it becomes saturated. A direct contact between leaves and soil is not necessary.

In the next few experiments the ability of a plant to absorb moisture from a moist soil, and to transport this moisture, and build up a dry soil will be considered.

A culture pot similar to that shown in figure 8, was planted with 12-day-old wheat seedlings, whose roots reached to the bottom of the pot. The pot was filled about three-fourths full of soil which was then wet to above the optimum. Warm paraffin-beeswax mixture was then poured over the top of the soil, around, and between the roots. The top one-fourth of the pot was then filled with moist sand, and the culture allowed to grow for several days until the plants were well established.

The sand layer was then removed, the roots brushed clean, and soil of 8.0 percent moisture, poured in around the roots. Then the top was again sealed with paraffin.

After standing for 7 days the top layer was removed, and a moisture determination of the soil made. The top layer had increased in moisture from 8.0 to 16.9 percent, representing a total of 19.4 grams of water, which had been absorbed from the moist soil, transported, and added to the dry soil.

Control pots without plants, but with the same arrangement of moist and dry soil, and paraffin partition, were run at the same time, but no appreciable build-up of the dry soil was obtained.

A great many experiments, similar to the one just described, but varying in technique and in the arrangement of soil layers, were made, and almost always evidence was obtained which indicated that a plant can absorb water from a moist soil, transport the water and build up the moisture content of a dry soil.

EXPERIMENTS IN THE FIELD WITH CORN PLANTS

During the latter part of the growing season of 1929, large, and almost mature corn plants were used to advantage. As is well known, when corn approaches maturity and comes into full tassel, it develops aerial, or "brace" roots, from several nodes near the base of the plant. When these roots emerge from the stalk and grow downward, they have chlorophyl, and they also develop a tough coat which protects them from desiccation. In dry climates, when the growing tip touches the soil, or in humid climates, even before actual contact takes place, the nature of the root changes. The growing tip becomes tender, opaque, and moist, and oftentimes a drop of water, or a thin fluid, may be seen suspended from the end of the root, and encased in a membrane. When the root touches the soil, a small wet area is formed. This phenomenon is noticeable especially in the early morning while the atmosphere is still humid. When the brace root enters the soil, many laterals develop near the tip, and these grow very rapidly.

In these experiments, long brace roots, which had just reached the soil, but had not developed laterals, were selected, a small excavation was made in the soil beneath the roots, and two or more roots were carefully inserted into small glass jars, as is shown in figure 9. Air-dried soil, or soil with moisture content at or below the wilting percentage, was then poured into the jar, and packed around the roots. The opening was then sealed with warm paraffin-beeswax mixture, the jar covered partially with soil, and an oilcloth apron fitted around the stalk, and over the jar to guard against the possibility of rain.

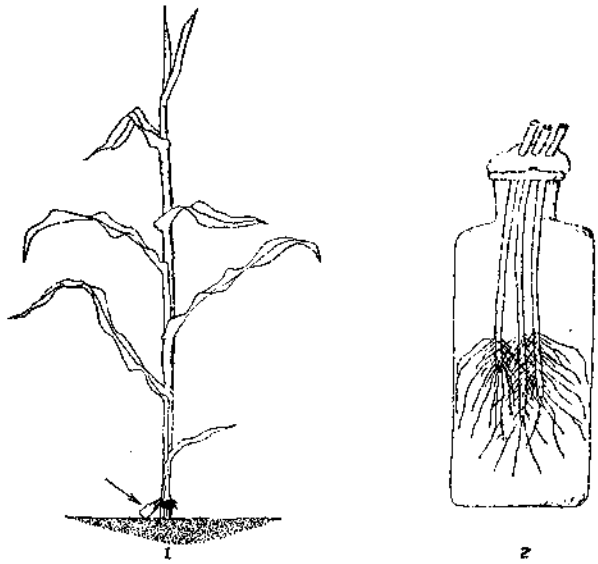


Fig. 9.—A corn plant and brace roots.

Occasionally the roots would stop growing when so treated, but in a great majority of cases, laterals would develop in the course of several days, and a mat of small roots would form inside of the jar. (Fig. 9-2.) A build-up of soil moisture in the jar was nearly always obtained. This build-up was slow and small with some cultures, and rapid and fairly large with others. A decided tendency to build up to near, but not above, the wilting percentage was noticed. If the soil is first made up to the wilting percentage, and then placed in the jars, this percentage is usually maintained. The lateral roots inside the jars were covered with root hairs, which suggested feeding roots, and some data have been obtained upon the absorption of nutrients by these roots. These root hairs will develop in a soil which is air-dry when placed in the jar. It is noteworthy that, whenever a growing root tip approached the glass, from the inside, a small moist zone of soil could be detected, even before the root appeared in view. Evidently the root tip was exuding water, which kept a moist zone of soil in front of, and in direct contact with, the elongating root. Often, during, or directly after a rain, the build-up was very pronounced.

These experiments could be conducted for a short period only, due to the ripening of the corn and to the approach of frost. They were, however, very suggestive of further opportunity for valuable work.

THE PLANT AS AN EQUALIZER

If a plant, when part of its roots are in contact with water, will build up the moisture content of a dry soil until the wilting percentage is reached, and if the build-up then stops, it might be expected that the same plant, if placed in a moist soil, or in a soil at the optimum moisture content, with part of its roots in water, should reduce the moisture content of the soil to the wilting percentage. This phenomenon is illustrated in the following experiment.

Five pots of Mission soil were prepared, with varying percentages of moisture, and 25 10-day-old wheat seedlings were placed in each of these pots, with a portion of their roots in water as is shown in figures 3 and 4. The plants were sealed in, as has been described, weighed, and kept under observation for 6 days. As mentioned before, the wilting range of this soil is between 16 and 19 percent. It was planned to have pots 1 and 2 with soil far below the wilting range, pot 3 with a soil at the lower limit of the wilting range, and pots 4 and 5 with plenty of available moisture.

TABLE III.—ABSORPTION AND BUILD-UP OF MOISTURE IN SOILS.

Pot	Percent moisture	Gain or loss in weight of pots		Transpiration
		Gain	Loss	
1	Dry	21.0 gms.	0.0 gms.	41.0 gms.
2	5.5	19.0 gms.	0.0 gms.	31.0 gms.
3	16.0	6.0 gms.	0.0 gms.	39.0 gms.
4	24.0	0.0 gms.	14.0 gms.	39.0 gms.
5	38.0	0.0 gms.	10.0 gms.	45.0 gms.

It will be seen that, although the plants in all the pots had access to free water, they did not act alike with reference to the moisture in the soil. The percentage of moisture in the dry soils, pots 1, 2, and 3, was built up considerably, while there was a reduction of moisture in both of the other pots. The plants were transpiring freely, as shown in the table. In pots 1, 2, and 3, more water was taken up from the water reservoir than was used for transpiration purposes. This difference was used in the build-up of the dry soil. In pots 4 and 5 less water was taken from the reservoir than that used for transpiration, and this difference in water was obtained from the moist soil.

Evidently, a plant can absorb moisture from a wet soil, or a subsoil, transport the water and build up the moisture content of a dry or surface soil. Furthermore a plant may absorb moisture from a soil which is above the wilting percentage, and reduce the moisture in the soil to the wilting range, although some of the plant roots may be in contact with free water, at some distance away. From the Mission soil, which has a wilting coefficient of 19, the plants usually absorb enough moisture to lower the percentage to 17.5 or 18. When placed in the same soil with a moisture content of 16, the plants usually build up the moisture content to about 17.

The plants in the moist soil were, of course, the most thrifty and, therefore, transpired the most water.

Although this experiment was duplicated frequently and although the results were very satisfactory, it was found difficult to obtain any one set of weights which could be plotted in a curve. In figure 10, is shown a graph which is representative of a compilation of data only, and is presented to illustrate the tendency of the plant to bring about moisture equilibrium in the soil.

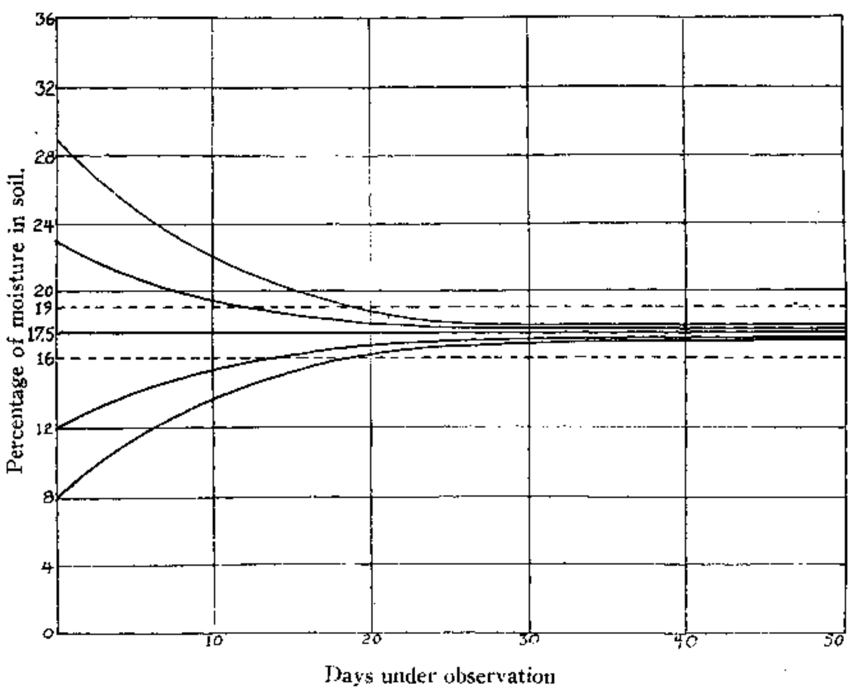


Fig. 10.—Graph illustrating the tendency of a plant to bring about moisture equilibrium in a soil.

In this graph the percentages of moisture in the soil of five culture pots are plotted against the days during which the cultures were under observation. The curves represent the gradual gain or loss in moisture of the soils due to the growth of the plant. It will be seen that, when the plants were placed in soil below the wilting percentage, there was a gradual build-up until the wilting range was reached, while in the soils above the wilting percentage there was a gradual reduction of moisture.

REDUCTION AND BUILD-UP OF SOIL MOISTURE AS SHOWN BY THE SAME PLANT

In the following experiment, the same set of plants was used to show the absorption of moisture from a wet soil, and the build-up of a dry soil.

Two culture pots were prepared, as has been described before, with soil at 33 percent and 5.5 percent respectively. The pots were weighed, and kept under observation for 2 days. There was a loss of moisture from the wet soil, and a build-up in the dry soil, as shown in Table IV. A hole was now cut into the side of pot 1 with a cork borer without disturbing any of the seals, and the moist soil removed. The pot was then filled with dry soil and the hole sealed with paraffin-beeswax. Pot 2, which had been dry during the first period, was now brought up to a moisture content of 33 percent, the two pots weighed again, and kept under observation for 4 days. The data for both periods are shown in Table IV.

TABLE IV.—ABSORPTION AND BUILD-UP OF MOISTURE IN SOIL AS SHOWN BY THE SAME PLANTS.

	Culture	Percent moisture in soil	Gain or loss in weight of pots		Transpiration
			Gain	Loss	
First period	1	33.0	0.0 gms.	12.0 gms.	39.0 gms.
	2	5.5	8.0 gms.	0.0 gms.	41.0 gms.
Second period	1	Dry	8.0 gms.	0.0 gms.	60.0 gms.
	2	33.0	0.0 gms.	9.0 gms.	57.0 gms.

It will be seen from this experiment that the same plant will absorb or exude water, depending upon the moisture content of the soil which is in contact with the roots.

THE SUCTION FORCE OF A PLANT

The ability of a plant to absorb water, or its suction force, is not a constant for all parts of the plant. The pull may be as low as 4 atmospheres at the root tip, and as high as 100 atmospheres in the above-ground parts of certain plants (3, 4, 7). In the case of tall trees, the force required to lift water through the cells from a root tip 20 feet below the surface of the soil to the transpiring leaf 80 feet, or more, above ground, must be very great. Assuming that the suction force at the extreme root tip is due almost entirely to osmotic pressure, this pressure must be determined by the concentration and nature of the cell sap and the soil solution. In other words, at the root tip, the solutes or salts in solution, whether dissociated or not, determine largely the power of the plant to absorb moisture from the soil. However, most colloids like gelatine, insoluble bodies like glue, or even cellulose and sponges, have the power of absorbing water. The suction force of any part of a plant depends largely upon what compounds are met with in that particular part. There is probably a minimum amount of such bodies at the root tip, and therefore the lowest suction force, and a maximum amount in certain parts of the above-ground tissue, where the suction force is greatest.

It has been the observation of the writer that the rapidity of the build-up in dry soils probably depends partly upon the distance of the dry soil from the moisture supply. This would indicate that the roots close up to the base of the plant, or the short roots, probably have a greater suction force than the long ones.

These observations are mentioned only in order to emphasize the role of the plant as an equalizer of forces. The plants in culture 5, Table III, were growing with their short roots in damp soil, and the ends of their long roots in free water. These plants absorbed and transpired 10 grams of water from the soil, and 35 grams from the water reservoir. The soil at 38 percent moisture had an adhesive force of one atmosphere which had to be overcome by the plant, while the cohesive force in the free water was negligible. The plant invariably takes the line of least resistance, and does the least possible amount of work, threfore had all other factors been equal, it probably would have absorbed all of its moisture from the free water, and none from the soil. However, it absorbed water from both the soil and the reservoir, and this prenomenon indicates that probably two or more factors were operating. Unquestionably, the tendency of the plant is to equalize all resistant forces, and the degree of the resistance, under the above mentioned conditions, between the moist soil of this particular culture and the free water, may be represented roughly, by the proportion of 10 to 35.

If the wilting percentage of a soil represents equilibrium between the suction force of the plant, and the attraction forces of the soil, the distance between the absorbing root tip, and the transpiring tissue may be of more importance than it is supposed to be.

These observations are suggestive of much more work.

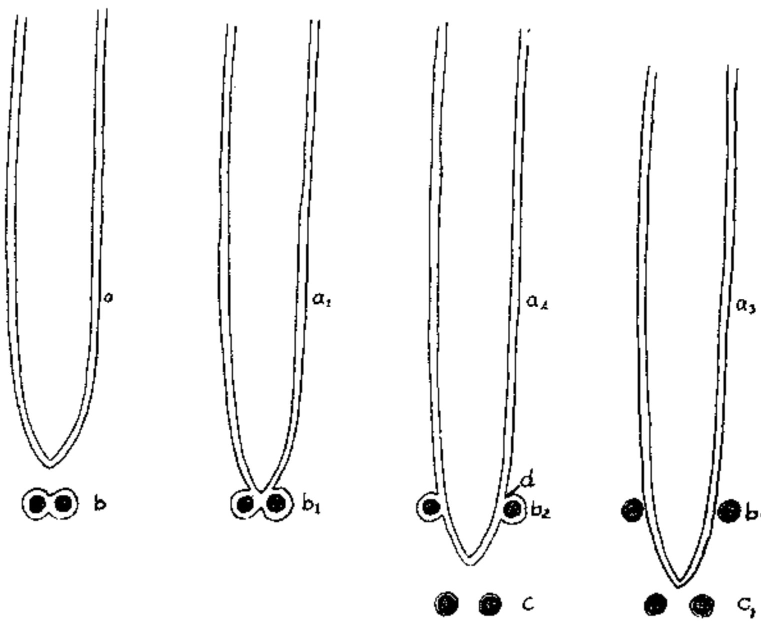


Fig. 11.—A root tip as it elongates in a soil at wilting percentage.

ROOT ELONGATION AT THE WILTING PERCENTAGE

It has been shown by Thomas (8), that the thickness of a soil film at the wilting percentage, is about equal to the total diameters of 100 molecules of water. The absorbing area of the root is covered also by a film of water, the thickness of which cannot exceed that of the soil particle with which it is in contact. A root, when elongating in a soil, tends to assume a rigid position, and it approaches and makes moisture contact with a soil particle by the addition of new cells. These new cells have a suction force equivalent to 5 to 15 atmospheres. In all probability the force is usually much nearer 5 than 15 atmospheres.

In figure 11 is shown a series of graphs illustrating the approach of a root to soil particles. A root, (a), is shown approaching two soil particles, (b). The particles are at equilibrium, and covered with a film 100 molecules thick. The outer circle of molecules surrounding these particles are held by an adhesive force of 4 or 5 atmopsheres, but the adhesive force increases rapidly as the soil particle is approached, until at the innermost layer, the force may amount to 25,000 atmospheres. It should be remembered that the force of adhesion which is exerted upon the innermost layer of molecules is the same, whether the soil is air-dry, at the wilting percentage, or at the saturation point. No root tip can endure 1/100 part of the pressure which is exerted upon the inner layer of molecules, and for this reason the absorbing root tip can never come in actual contact with the soil particle and live. It must be separated from the particle by a film of water of about the thickness of 100 molecules.

If the root is elongating by the addition of new cells, it will come eventually within the zone of influence of the soil particles, and a condition represented in figure 11, (a_1), will be produced. Instead of two films, one surrounding the root and the other the soil particles, the film will be continuous from the soil to the root.

If the pull of the soil is now balanced exactly by the suction force of the root, no absorption of water by the plant can take place, however, absorption of nutrient ions may go on, and there is nothing to interfere with further elongation of the root.

As a matter of course, figure 11 does not give an idea of the relative sizes of the root and the soil particles. The diameter of the root is equal to that of millions of soil particles. The soil particles lie close together, and must be pushed aside as the root elongates. Such a condition is shown in figure 11, (a_2). The force which is required to push the soil particles is transmitted from the root to the moisture film, and from the film to the soil particle. At no time does the root actually touch the soil particle. A film of water, at least 100 molecules thick, must intervene between the root and the particle. In reality, the soil particles are pushed apart by the force of adhesion, and the phenomenon is much the same as that observed in the swelling of soils when water is added to them.

Assuming that the root has now reached a soil horizon which is slightly below the wilting percentage, the particles, (c), are encountered. These particles are covered with a film of water, probably not more than 50 molecules thick. The adhesive force of these films is very great, no new root cells can endure the pressure, so root elognation ceases. The root, however, is still covered with its film. If desiccation, due to surface evaporation, is taking place slowly in the soil, the plant may exude enough water to keep the soil which is in contact with the root tip at the wilting percentage. This is shown in the work which has just been described. If, however, surface evaporation is taking place very rapidly, the plant may not be able to accommodate itself to such a condition, and the thickness of the soil films may decrease to a point where the pressure cannot be endured by the roots. The root then will lose a small amount of water, it will shrink slightly, and the film contact will be broken at (d).*

*The author is indebted to W. T. McGeorge for this suggestion.

A film of less than 100 molecules in thickness will then spread over the soil particles, and there no longer will be a moisture contact between the root tip and the soil.

The absorbing area of the root will now be relieved of the stress of the powerful adhesive force of the soil and, surrounded by an atmosphere of a high relative humidity, although dormant, it may remain alive for a long time, or until the next rain or irrigation. Such a condition is shown in figure 11, (a_3). When in moisture contact with soil particles, a root tip must be covered at all times with a film at least 100 molecules thick, but when this moisture contact is broken, the root film may be reduced to a thickness of much less than 100 molecules.

WATER MOVEMENT AND NUTRITION OF PLANTS

The discussion of plant-soil relationship has thus far been confined largely to the study of water movement. The movement of water in soils, however, is closely associated with the nutrition of plants. Mineral plant foods must be in aqueous solution, that is, they must be dissolved in the soil solution before they are available. It has been shown already that plants possess the power to absorb water wherever it is available, and to return this water to the soil wherever it is most needed. As far as water alone is concerned, this is only a temporary expedient, which enables the plant to tide over periods of drought. Whether the water, which is returned to the soil, can dissolve, and render plant foods available, now will be considered.

NUTRITION OF PLANTS AN ELECTRICAL PHENOMENON

The nutrition of a plant is not thoroughly understood. In all soils which are capable of supporting plant life of a higher order, the film water tends to become in equilibrium with the soil particle, and saturated with respect to its more or less soluble constituents. This film constitutes the soil solution, and it is from the soil solution that the plant derives its mineral nutrient material. As has been mentioned before, every absorbing surface of the plant root is covered also by a film of water, so a direct water contact exists at all times between a live root and the soil particles.

When a nutrient salt, potassium chloride for example, goes into solution, the salt ionizes partially. The potassium chloride splits into two parts, namely, potassium, (K), which carries a positive, and chlorine, (Cl), which bears a negative charge. Owing to the low concentration of the soil solution, the nutrient salts are ionized almost completely. It is fairly well established that the plant feeds upon ions, and not upon the unionized salt.

When a salt is ionized, the ions move freely in solution, not by diffusion, but by differences in potential. Nutrient salts remain in solution in the soil even though the moisture is reduced to the wilting percentage, or much lower. These facts are of much importance in the study of the plant-soil relationship at and below the wilting percentage. If a plant feeds upon ions, and if bodily movement of water is not necessary for the movement of these ions, and, if a direct water contact exists between the plant root and the soil, it is not unreasonable to assume that a plant can absorb nutrient ions from a soil after all movement of water has ceased.

Several years ago the author advanced the theory that the nutrition of plants is an electrical phenomenon, and since that time a considerable amount of data has been accumulated which goes to prove the theory correct. The demand for plant food originates within the tissues, and is probably carried to the absorbing tip of the root, through colloidal compounds of the sap which bear plus or minus charges. If potassium is needed as a permanent constituent by the growing leaf tissue, the ion, (K), with its positive charge is removed from the sap by the protoplasm, and used in building the final compound. This leaves the colloid with a negative charge, the position of the K ion is filled by replacement, and the charge is transmitted, through the cells of the plant, and appears at the root tip. A chemical combination will take place, and a molecule will be formed which will be in equilibrium with respect to positive and negative charges. The potassium in this way may be transferred from the soil film, through the root and the cell sap, to the extreme tip of the growing tissues, without a bodily movement of water.

If a demand for nitrate (NO_3) originates within the tissues, this demand will be carried to the root tip as a positive charge. If sodium nitrate ($NaNO_3$) exists in the soil solution, ionized as plus Na and minus NO_3, the NO_3 ion will migrate to the positive charge of the root tip. Such is the substance of the theory that the nutrition of plants is an electrical phenomenon, and its application to the growth of plants in a soil at the wilting percentage is obvious.

The tendency of the plant is to maintain equilibrium in its cell sap, and the tendency of the soil solution is to remain in equilibrium both with the plant and with the solid particles of the soil. As there is a direct water connection throughout, in all probability, ions migrate through the soil film to the plant root, and from the root to the growing tissues as they do from one pole to another in an electric battery.

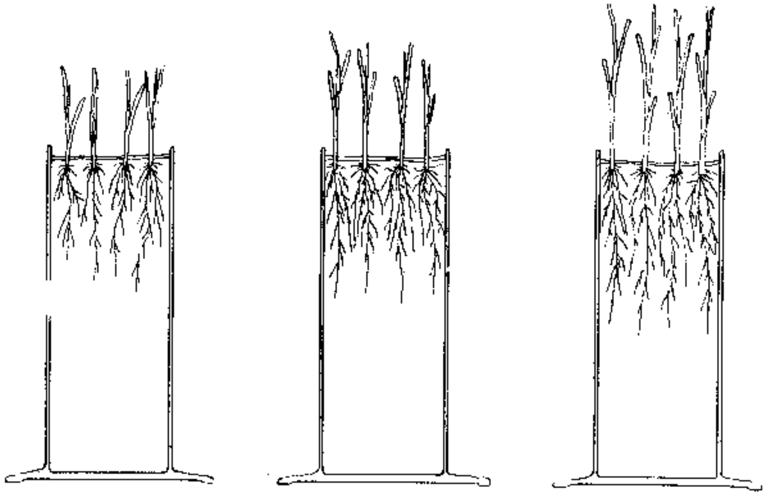
The plant root is never in direct contact with a solid soil particle, and cannot approach nearer than the diameters of 100 molecules of water.

However, if a direct water connection exists, a plant may feed at relatively long distances from the source of supply of the nutrient.

ABSORPTION OF NUTRIENTS FROM THE SOIL

In measuring the absorption of nutrient material from a soil the ion potassium was used in preference to phosphorous or nitrogen, for several reasons. The salts of potassium are very soluble, they are highly ionized, they do not oxidize or reduce as readily as salts of nitrogen, and they do not precipitate in the soil to the same extent as the phosphate ion. The plant feeds heavily upon potassium during the early stages of growth, and the analysis for this element is easily and quickly made. In a general way, what is true of the absorption of potassium is true also for the other nutrient ions.

If wheat seedlings are grown in distilled water for 2 weeks or more, and are then ashed and analyzed for potassium, the analysis will indicate the potassium which was contained in the original seeds. This amount will vary, on account of the difference in size and composition of the seeds. In the course of this work, control water cultures were grown and analyzed occasionally, and the average composition was .0060 grams of potassium for every 25 tops, and .0025 grams for 25 roots. In order to determine the amounts of potassium absorbed by seedlings from a soil, it will be necessary to subtract the amount in the original seed from the total amount found in the plants. Usually the tops only were analyzed on account of the difficulty of removing the soil which adhered to the roots.



1 2 3

Fig. 12.—Three culture jars of soil at different moisture percentages.

In handling dry seedlings, great care must be taken in order to avoid loss of potassium. The potassium salts in dry tissues will be dissolved and probably lost if the plants are wet. The salts may crystallize on the surface of the dry leaf, and even may be shaken off or blown away by air currents.

Twenty-five 10-day-old wheat seedlings were planted in each of three glass cylinders, holding 1,400 grams of soil each. (Fig. 12.) The soil in cylinder 1 was made up to 18 percent moisture, or about 1 percent below the wilting coefficient. Cylinder 2 was made up to 22 percent or about 3 percent above the wilting percentage, and cylinder 3 was made up to 28 percent. After planting, the soil was sealed over the surface with a layer of a mixture of paraffin and beeswax, about 1 cm. thick, to prevent surface evaporation. The plants were kept in a light, open room, and were not covered. The seedlings in No. 1 wilted in a few hours, those in No. 2 grew for several days before wilting, while those in No. 3 grew for 8 days, or until they were removed from the soil at the end of the experiment. The parts of the plant above ground were then harvested, dried, ashed, and analyzed for potassium. The results are shown in Table V.

TABLE V.—THE ABSORPTION OF POTASSIUM BY WHEAT SEEDLINGS FROM SOILS WITH DIFFERENT PERCENTAGES OF MOISTURE.

Culture	Percent moisture	Grams K in 25 plants
1	18	0.0050
2	22	0.0086
3	28	0.0141

Analysis of control plants which were grown in distilled water, showed practically the same amount of potassium as those in culture No. 1. Evidently, there was no absorption of potassium by the plants from the soil in cylinder 1. The plants in No. 2 did not exhaust all the available moisture in the soil, but the rate of movement of film water was slow, transpiration was rapid, and the roots were in contact with a relatively small amount of soil, so the plants wilted, and gradually died, before all of the available moisture could reach the roots. However, there was a definite increase in the amount of potassium in the plants, due to absorption from the soil. The rate of water movement in culture 3, was rapid enough to enable the plants to grow for at least 8 days, and a decided increase in the absorption of potassium was obtained.

This experiment was repeated with corn seedlings, and the results are shown in Table VI. The corn plants behaved very much like the wheat seedlings in the experiment just described.

Plants, when the entire root system is confined to a soil which is maintained at the wilting percentage, and with no source of water except that in the soil, will absorb very little moisture, and little or no nutrient ions.

TABLE VI.—THE ABSORPTION OF POTASSIUM BY CORN SEEDLINGS FROM SOILS WITH DIFFERENT PERCENTAGES OF MOISTURE.

Culture	Percent moisture	Grams K in 10 plants
1	18	0.0069
2	22	0.0084
3	28	0.0209

Many desert plants, and a few crop plants, however, have the power to store up water in their tissues, which water may be returned to the soil whenever necessary. As mentioned before, most crop plants either have tap roots or deep roots also, which grow down and into a soil horizon which is seldom reduced to the wilting range, and even though the feeding root zone may be reduced to the wilting percentage, a supply of moisture is usually available. What effect this subsoil moisture may have upon the absorption of plant food, in the "root-dry" feeding zone, will be noted in the following experiments:

ABSORPTION OF POTASSIUM FROM SOILS AT THE WILTING PERCENTAGE

Soil to which 200 parts per million of potassium nitrate was added, was made up to 19 percent moisture, and 2 paraffined, earthenware pots, holding 1,400 grams each were prepared. Twenty-five, 14-day-old seedlings were planted in pot No. 1, and sealed in with warm paraffin-beeswax mixture. Twenty-five other seedlings were planted in pot 2 with a portion of their roots in water, as shown in figure 5. These were sealed in at the top with paraffin-beeswax mixture and the roots were sealed with vaseline, plaster of Paris, vaseline and heavy-oil seals, as has been described. The plants in culture 1 wilted in a few hours, and died in a few days, but those in No. 2 made good growth. The cultures were kept under observation for 17 days, when the tops were cut off, dried, ashed, and analyzed for potassium.

A moisture determination was made of the soils in both pots at the end of the experiment. In making such moisture determinations, an effort was made to secure the soil from immediately around the roots. The moisture determinations, therefore, do not represent the average moisture content of the pot, but only of the soil which was very near the roots. In Table VII are shown the data of this experiment.

In these experiments the dry weights of plants are of little importance. There was some loss of water from the soil through the walls of the earthenware pots, and there were unavoidable errors in moisture determinations due to sampling, etc.

TABLE VII.—ABSORPTION OF POTASSIUM FROM SOIL AT THE WILTING PERCENTAGE.

Culture	Percent water		Dry weight 25 tops	Grams K 25 tops
	Before	After		
1	19.0	16.1	0.288	0.0052
2	19.0	20.5	0.572	0.0213

It will be noted that there was a reduction in the moisture content of No. 1, due probably in part, to evaporation from the sides of the pot. The apparent increase of moisture in No. 2 during the experiment probably was due to experimental errors. There was at least, no reduction of moisture in No. 2. The amount of potasium in the cultures is the most interesting feature. Evidently there was no absorption of potassium from the soil by the plants in culture 1, where no moisture was available. Assuming that the plants in No. 2 obtained .0060 gram of potassium from the original seed, and without considering the possible increase of potassium in the roots, which was not determined, it will be seen that the plants in No. 2 absorbed at least .0153 gram of potassium from the soil which probably was never above the wilting range during the entire period of growth.

In Table VIII is shown a duplicate of the experiment just described, except that these cultures were grown in porcelain pots, (Fig. 3). With such pots it was found possible to eliminate the loss of water by direct evaporation almost completely. These plants were kept under observation for 24 days.

TABLE VIII.—ABSORPTION OF POTASSIUM FROM SOIL AT THE WILTING PERCENTAGE.

Culture	Percent water		Dry weight 25 tops	Grams K 25 tops
	Before	After		
1	19.0	19.0	0.680	0.0092
2	19.0	19.0	0.980	0.0335

The plants in culture 1 died in a few days, but those in culture 2 made good growth. There was no gain or loss in moisture in either of the two cultures. However, the difference in the amount of potassium in the ash was noticeable. The amount absorbed by the plants in culture 1 was very small, in fact the difference from the amount of potash in control water cultures may be accounted for by experimental errors. Assuming that 25 water cultures contained .0060 gram of potassium in their tops, the amount of potassium absorbed from the soil by plants in culture 2 and stored in the tops was about .0275 gram. This was far greater than any probable error. Evidently the plants were absorbing potassium from a soil which was never above the wilting percentage.

Such experiments as these were repeated many, many times, and while it was found impossible to duplicate the absorption of potassium in exact amounts, the outstanding fact was always evident,—namely, that a plant can absorb nutrient ions from a soil which is maintained constantly at the wilting percentage, provided a supply of water is available to at least a part of its root system.

It must be understood, however, that low percentages of moisture interfere seriously with the absorption of nutrients. A plant feeds much more readily in a soil at the optimum, than it does at the wilting percentage. The interesting fact is that it is able to absorb a relatively small amount of nutrient material from a soil at the wilting percentage.

The application of this phenomenon to practical agriculture is yet to be proved. Plants with a tap, or deep root system, may draw moisture from one soil horizon for transpiration purposes, and may absorb at least a portion of their plant food from another horizon when no moisture is available.

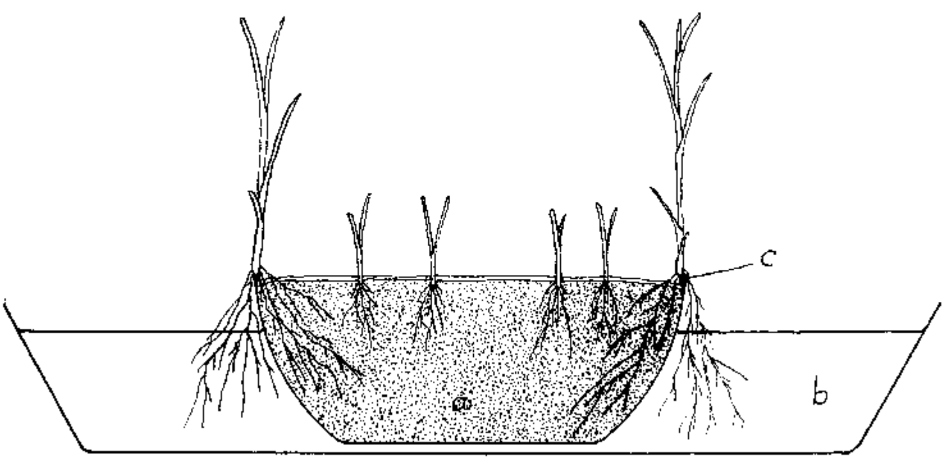


Fig. 13.—A culture with one-half of the roots of some of the plants in soil, and the other half in water.

OTHER METHODS OF APPROACH

Many changes in technique were made during the progress of the work, and results as positive as those just described were often obtained.

In figure 13 is shown an illustration of the different arrangement of seedlings. A small, enameled bowl (a) was filled with soil at the wilting percentage, or 19 percent, and 25 seedlings were planted in a circle near the center of the pot. Twenty-five other seedlings were planted around

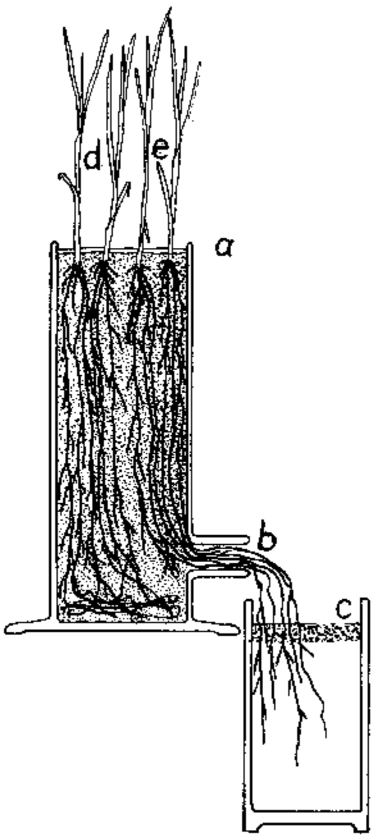


Fig. 14.—A culture jar with the roots of one-half the plants confined to the soil, and the ends of the other half of the plants with access to free water.

the rim, with one-half of their roots in the soil. The bowl was then placed in a large pan of water (b), so that the other half of the root systems of the outer row of plants was in water. A thick coat of vaseline was applied to the base of the outer row of plants (c), and a paraffin-beeswax seal poured over the top of the soil. One hundred parts per million of sodium nitrate was added to the water in the pan, in order to stimulate growth in the seedlings. The plants in the inner row wilted, and died in a few days, but those in the outer row made good growth. Usually the moisture in the soil was reduced from 19 to 17.5 percent or lower. The plants in the inner row made no root growth, and absorbed no potassium from the soil, but the plants in the outer row made a good growth and developed a good root system in the soil, which was never above the wilting percentage. The outer plants absorbed appreciable amounts of potassium from the soil.

In figure 14 is shown another modification of methods.

In this experiment, 50 seedlings were planted in the same cylinder in soil at the wilting percentage. The roots of 25 of the plants were confined to the soil (d), while the ends of the roots of the other 25 plants (e) were carried through an opening in the side of the cylinder and into a reservoir of water. The roots of both sets of plants were near, and often in contact with each other. The plants were sealed in with paraffin-beeswax at (a), and the roots sealed with vaseline at (b) and with oil at (c).

In experiments under such conditions it was noted that the plants when all of their roots were confined to the soil (d) did not wilt and die as they would have done if the other set of plants had not been present. Evidently the second set of plants (e) absorbed moisture from the reservoir (c), and transferred it to the soil. A part of this moisture was then made use of by the first set of plants. If the soil is made up to moisture content slightly above the wilting percentage before planting, very decided results in the absorption of potassium may be obtained.

Experiments of this nature require a great deal of attention.

SUMMARY

1. The contact of moisture film is continuous from the soil to the growing plant at all soil moisture percentages, above the wilting percentage.

2. The wilting percentage of a soil is assumed to be the state of equilibrium which exists between the suction force of the plant, and the adhesive forces of the soil.

3. The wilting percentage of any soil lies within a zone, or range, the width of which depends upon the type of plant, upon root distribution, length of root, rate of transpiration, and other factors.

4. The available moisture in a soil is that water which is held by the soil with a force of less than the suction force of the plant, or a force of less than about 5 atmospheres.

5. The plant is presented in the role of a great equalizer of certain natural forces. If the attraction of the soil for water is less than the suction force of the plant, water will move from the soil to the plant. If, however, the attraction of the soil is greater than the suction force, water may move from the plant to the soil, and thus equilibrium may be maintained.

6. A plant can absorb water from a moist soil, or subsoil, transport this water, and build up the moisture content of a dry soil.

7. A plant is able to absorb water from a soil at optimum, and reduce its moisture percentage to the wilting range, and at the same time build up a dry soil to the wilting range.

8. Plants are able to draw nutrient materials from a soil which is maintained at the wilting percentage.

9. Nutrient ions are probably taken up by the plant as electrical charges. No bodily movement of water is necessary for the movement of ions. As a direct water contact exists between the plant and the soil, nutrient ions may move from the soil to the plant, even after all soil water movement has ceased.

10. A plant may absorb moisture from any soil horizon where water is available, for example a subsoil, and transport this moisture to another horizon, where moisture is scarce, for example, the surface soil. It may there exude this water, dissolve, and absorb certain amounts of nutrient materials.

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