

WATER AS A FACTOR IN THE GROWTH OF PLANTS.

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Of all the factors influencing the growth of plants, water is beyond a doubt one of the most important. Plant physiologists have long recognized this fact, but it is only recently that farmers, fruit growers, and others interested in the growth of crops have come to fully realize its importance. As an indication of the growing interest in this subject we may cite the agitation now being made in behalf of irrigation. Irrigation at one time was considered for the most part in connection with the production of crops in the arid regions or in sections where the yearly rainfall is not sufficient for the best development of our agricultural crops. Now nearly every section of the country is more or less interested in the subject. In Florida, where the average yearly rainfall is about 55 inches, or nearly three times as much as in some sections of the West, thousands of dollars are being spent every year for irrigation. The chief reason for this is that although the yearly rainfall is sufficient to grow any ordinary crop, yet it is distributed in such a way that the best conditions for plant growth are not furnished. It is here that irrigation plays an important part, for if just the right amount of water can be furnished at the proper time, other conditions being favorable, the plant immediately responds and a better growth is the result. The whole problem of the proper use of water and its effect on the plant is a complicated one, and until it is better understood by farmers themselves we can not hope to attain the highest development in agricultural pursuits.

The plant may be likened to a complicated and exquisitely sensitive machine, depending largely for its ability to do work on four factors, namely, heat, light, food, and water. If these are furnished in just the right amounts and at just the right time there is harmony in all parts of the machine, and as a result the greatest amount of work is performed; if, however, any one or all of the factors are deficient or excessive, then the perfect working of the machine is destroyed, and its ability to do what is required of it is impaired. In other words, certain diseases appear; or if the plant does not, strictly speaking, become diseased, the growth of the various parts may be unbalanced, resulting in a development which is so different from what is wanted as to have little practical value. Thus leaves and wood may be produced

at the expense of the fruit, or the reverse may be the result of the unbalanced condition of the factors mentioned.

In field culture, heat and light can not well be controlled, but food and water may be to a certain extent, the latter either directly, by supplying it artificially, as in irrigation, or indirectly, by selecting soils having a capacity for moisture best suited to the crop or crops to be grown. Our object, however, is not to discuss these questions, but rather to point out the important part that water plays in nearly every vital process of the plant, in the hope that what is said may awaken the interest of farmers, fruit growers, and others in a much-neglected line of study. We shall not give an exhaustive treatise on the subject, nor attempt to present any specially new facts. Our purpose is simply to bring together some of the knowledge already familiar to vegetable physiologists but as yet little known to those interested in the practical side of plant production.

WATER IN GREEN PLANTS.

The fact that green plants lose a large proportion of their weight in drying is familiar to all. This loss is made up largely of water, the amount of which, compared with the dry substance found in plants, is very great. Thus in every 100 pounds of fresh meadow grass there is found 60 to 80 pounds of water. In 100 pounds of red clover there is often as high as 86 pounds of water, while in such plants as lettuce, cucumbers, cabbage, onions, etc., there is often as much as 95 to 98 pounds of water in every 100 pounds of fresh material. The seeds of plants do not contain as much water as the leaves, stems, and other vegetative parts. Wheat, rye, and oats contain about 14 per cent each, while corn contains about 12 per cent. This comparatively small amount of water contained in the seed is one of the reasons why the latter will remain dormant so long. As soon as the seeds are brought into a moist place, and other conditions for growth are present, they absorb large quantities of water and soon begin to germinate.

It is impossible at ordinary temperatures to dry out all the water held by plants. Most air-dried plants contain as much water as ordinary seed, and this can be removed only by a prolonged exposure to high temperatures.

We see from the foregoing that water forms a large proportion of the actual weight of all plants, and its importance, therefore, in this connection is at once apparent.

RELATION OF ROOT DEVELOPMENT TO WATER SUPPLY.

All our agricultural plants obtain their water exclusively through the roots. That leaves do not absorb water to any appreciable extent under normal conditions of growth has been so fully demonstrated as to need no discussion here. Accordingly, it needs little argument to prove that a well-developed root system is of the highest importance

to the welfare of the plant. There is usually a rapid development of these organs in the early period of growth, and if the proper moisture conditions are present at this time the chances are that a root development favorable to the future growth of the plant will be attained. It should be pointed out, however, that the development of the roots and the form which they may take will be modified by other conditions, and it may be possible to take advantage of these in order to insure a proper water supply as the plant grows older. For example, the distribution of food in the soil may have a very important bearing on the production of roots as well as the position they assume. An interesting experiment bearing on this point was made by Nobbe, a German investigator. He grew a number of corn plants in poor clay soil, contained in glass cylinders. In each cylinder of soil a certain amount of fertilizer was put, in each case in a different position, so as to observe its effect on the growth of the roots. When the plants were nearly four months old the vessels were placed in water and the soil carefully washed from the roots. They were then suspended in water and took nearly the same position they had in the soil. Where the fertilizer had been uniformly mixed with the soil the roots grew equally through the whole mass. Where the fertilizer was placed in a horizontal layer about an inch below the surface the roots formed a mat in this layer, those that extended through being slender and not greatly branched. Where the fertilizer was placed in a horizontal layer at about half the depth of the vessel there was a spheroidal expansion of the root system at this point. Where the layer was placed at the bottom of the vessel the roots were slender and not much branched above, but at the bottom they formed a mat. When the fertilizer was placed around the cylinder of earth next the sides of the jar the external roots were greatly branched, forming a cylindrical nest, but the inner roots were not much developed. When the fertilizer was put in a central vertical core the inner roots were greatly developed, while the outer ones were much less so.

These facts and others of a similar nature show the importance of studies in this direction. It would be especially valuable in the West, and in other sections of the country liable to great variations in the water supply, to be able to control to some extent the character of the root systems of our agricultural plants. If this could be done by methods of cultivating the soil or of distributing the food, where food is used, there is no doubt that the water supply could in a measure be controlled. In this connection it is also important to bear in mind that the best development of the roots and of the plant as a whole is attained only when the water supply approximates a certain amount. This amount will vary with different plants, soils, temperatures, etc. For example, roots produced in very wet soil will not live when the latter dries out to any extent, and in consequence the plants grown under such conditions will suffer. On the other hand, roots produced in dry

soil will not live long if the latter is made excessively wet for any length of time. All these things of course have a marked effect on the development of the plants and the various parts of the same. The total product is not only made to vary by the amount of water at the disposal of the plant, but the proportional amounts of the various organs are also made to vary. Thus in the case of wheat, rye, barley, and other similar plants, a certain amount of water will not only produce the greatest yield of both grain and straw, but will also influence growth so as to give the maximum amount of grain with the minimum amount of straw.

It has been found that when the water in a soil amounts to 80 per cent or more of its water-holding capacity it is detrimental to the plants. Ordinary plants do best when the water in the soil amounts to from 40 to 60 per cent of the water-holding capacity. The water-holding capacity of a soil is the amount of water that a given weight, say 100 pounds, of the soil will contain when all the space between the grains of soil is filled with water. For example, a cubic foot of a very sandy soil has been found to contain about 40 per cent by volume of air space; when all this space is filled with water the sand will contain four-tenths of a cubic foot of water. A hundred pounds of such soil, when all the space between the grains is filled with water, contains about 20 pounds of water. In the same way wheat soil has been found to contain about $31\frac{1}{2}$ pounds of water in every 100 pounds of the fully saturated soil. The amount of water in this soil most favorable to the growth of wheat is from 40 to 60 per cent of $31\frac{1}{2}$ pounds, or from $12\frac{1}{2}$ to 19 pounds per 100. The water-holding capacity of heavy clay soils is about 44.2 pounds of water in 100 pounds of saturated soil. The most favorable condition for plant growth in such soils is when they contain from 16 to 24 pounds of water in 100 pounds of the saturated soil.

It is easy to see why the conditions in a soil having all or nearly all the space between the grains filled with water are detrimental to plant growth. Under such conditions the roots are immersed in water and the soil is very poor in oxygen. On the other hand, when only a part of this space is filled with water the roots are not immersed, and there is a sufficient supply of oxygen. These questions, however, more properly belong to the realm of soil physics, and therefore need not be discussed in detail here.

STRUCTURE OF THE PLANT AND HOW IT OBTAINS WATER.

In order to get a clear idea of the absorption of water by the plant and its movement in the same, it will be necessary to consider, very briefly, its general structure. In all the plants with which we are concerned the roots consist of a central axis of elongated, rather thick-walled cells and vessels, as shown in cross section in figure 12. Around this axis is a rather thick cylinder, composed of layers of soft, thin-walled cells (*p*), which have a great affinity for water. Surrounding

these and forming the outer covering of the root is the epidermis (*e*); many of the cells composing the latter grow out into relatively long projections, known as root hairs (*h h*). These adhere closely to the particles of soil and absorb the film of water adhering to them.

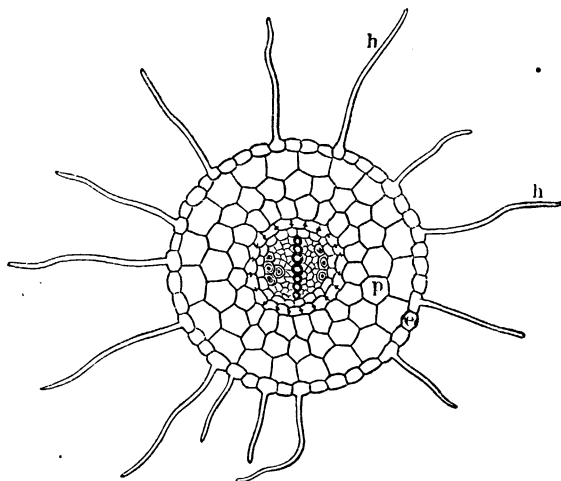


FIG. 12.—Cross section of root.

The absorption of water is well shown in figure 13, taken from Sachs's Lectures on the Physiology of Plants; *e*, on the right of the figure, is the

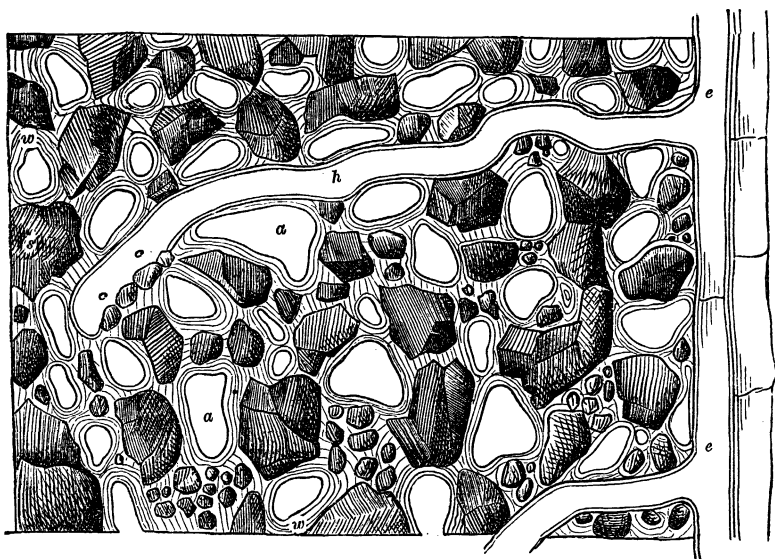


FIG. 13.—Root hair in the soil, showing absorption of moisture.

epidermis of the root; *h* is a root hair forcing its way in between the grains of soil, *s*, shaded dark in the drawing; the larger rounded white spaces, *a a*, represent air; and the wavy lines, *w*, surrounding the par-

ticles of soil and inclosing air bubbles, represent water held to the grains by surface attraction. All are greatly magnified. At the points marked *c* there is close contact of the root hair with the grains of soil. The root hairs, like the grains of soil, are also covered with a thin layer of water, and their walls are saturated with it. Wherever the particles of soil come very close together or touch, the spheres of water surrounding them unite at these points, thus forming a network of the water envelopes of the soil grains. Now, if there is no disturbance in the soil due to evaporation or absorption, this network of water will be held at rest by the attraction of the soil particles; but if any portion of

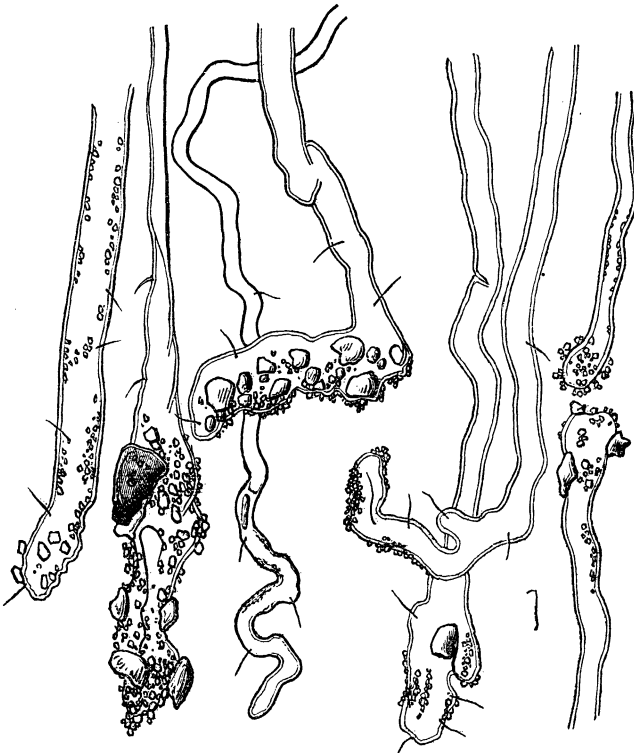


FIG. 14.—Root hairs.

it is removed, the soil particles that have less will immediately draw from those that have more, so that there will be a movement of water throughout the whole system toward the point where the water is taken away. We will now suppose the root hair, *h*, gives up a part of its water to the cells of the main root; it then absorbs water from the layers with which it comes in contact in the soil, and there is in consequence a movement of the entire water system in the soil toward the root hair until equilibrium is restored. It is evident from this that a plant may draw water from a much larger area of soil than that with which the root system comes in direct contact.

Figure 14 shows a number of root hairs cut from the root and highly magnified. Most of the soil particles have been washed away, but some adhere so closely that they can not be removed without breaking the hairs. This close connection is partly due to the dissolving action which the hairs exercise on the soil grains.

It must be understood that the water absorbed by roots is not pure, but contains in solution small quantities of all the soluble compounds in the soil; some of these are absolutely necessary to the growth and maturation of the plant. Ordinary well water contains all the substances absorbed by the plant in about the same degree of concentration in which they are found in the soil, viz, one to two parts of solid matter to one thousand parts of water. The plant does not necessarily absorb the solution in this proportion; it may absorb more or less, according to circumstances. It may absorb the compounds in the soil without taking up any water, or, on the other hand, it may absorb water without taking up the compounds, depending upon certain physical and physiological conditions. The compounds thus taken up are estimated in the plant as ash. The amount of ash varies greatly in different species and to some extent in different individuals of the same species. Furthermore, it may vary greatly with the age of the plant and the organ under consideration. The total amount, however, is usually very small compared with the gross weight of the plant. The amount seldom runs above 18 per cent (it is usually from 2 to 7 per cent) of the dry weight of the plant. However, it is absolutely necessary that the plant have certain parts of this material, and it can be obtained only as it is dissolved in water and absorbed through the roots. From the roots it passes by diffusion to all parts of the plant. In the parts of the plant above ground, i. e., the stem and branches, the woody portions form a framework which supports the other tissues, made up of more or less soft-walled cells. The outer layers of these cells form the epidermis or outer covering of the plant, and this is usually developed so as to protect the underlying cells from injury, especially through the loss of water.

Through the epidermis of the leaves and sometimes also of the stems, there are minute openings into the spaces between the inner cells of the leaf, for the cells in a plant in a general way may be likened to potatoes in a sack, touching only in places, though the union is relatively very much closer between the cells of a plant than it is between potatoes in a sack. The sack represents the epidermis, the potatoes the cells, and the spaces between the potatoes are comparable to the intercellular spaces.

Figure 15 shows a piece cut from a common leaf and greatly magnified; *u* is the upper and *l* the lower epidermis; the cells with the dark bodies, *c c*, within are the starch-manufacturing cells; *i i* are the spaces between them; the little oval openings, *s s*, in the lower epidermis are the breathing pores (stomata); at *s'* one is shown cut through, opening

into an intercellular space; the two cells bordering the opening are the guard cells.

The breathing pores allow the entrance into the plant of air and certain gases, which, through the intercellular spaces, come in contact with every cell. The intercellular spaces and the larger and older vessels are usually filled with air. The cells, however, are so closely in touch that water and whatever is in solution may pass readily from cell to cell by diffusion. If any cell lacks water, sugar, or any other material in solution it immediately takes it from neighboring cells, and these in turn take from others that have more, so that the equalization goes on throughout the whole plant, and different materials are moving toward the parts of the plant where they are used.

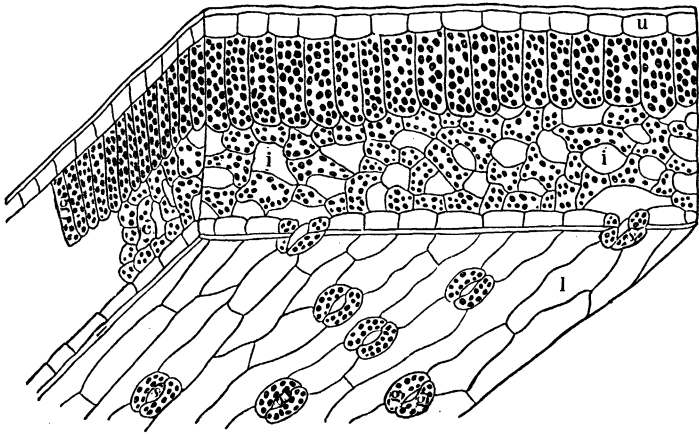


FIG. 15.—Section of leaf.

RELATION OF WATER TO GROWTH.

The growth of the plant is nothing more than the growth of the cells composing it. The cells may increase in number and they may increase in size. Supposing that the cells are supplied with all the necessary materials in solution required for growth, and that the external conditions are favorable, there is still one very essential condition—there must be a sufficient supply of water to keep every cell thoroughly distended. The cell at first may be compared to an elastic sack, but after a time its wall thus distended becomes more or less thickened, loses most of its extensibility, and the increase in size becomes fixed. If, however, before this occurs the internal pressure or turgidity of the cell is lessened by loss of water the cell shrinks in proportion to the decrease, and unless the pressure is again renewed, may become fixed in this smaller condition. This loss takes place as a result of evaporation from the foliage and other green parts of the plant, and goes on from the very beginning of growth. If the evaporation goes too far the cell will pass into a flaccid condition, which causes the plant to wilt

and unless water is furnished, so that the cells may again become turgid, the plant soon dies.

It is evident, therefore, that the rapidity of the increase in size of a plant depends on the degree of turgidity of the cells, other conditions being favorable. The turgidity may be just sufficient to keep the plant from wilting, in which case the growth will be very small. Plants may, therefore, suffer for water long before they show it by wilting. It has been observed that plants growing in certain kinds of sandy soils almost cease growing whenever in May or June there occurs a series of warm, rainless days, accompanied by dry winds. The development of young clover, for instance, on such soils will come almost to a standstill, but it will not begin to wilt for a long time. It wilts on stony ground first; then in a few days the whole field wilts, and the crop is destroyed.

On the other hand, plants may, under certain conditions, absorb too much water, not only filling and distending the cells, but filtering through the cell walls into the intercellular spaces; the plant then becomes water-logged and has a more or less transparent look. If this intercellular water is not removed by evaporation the plant soon suffers from lack of sufficient oxygen and carbonic acid gas. At other times too great turgidity causes abnormal swellings on the leaves and stems. The walls stretch so far that they break, the water escapes, and the cells dry up and die. Occasionally throughout the whole plant the turgidity is so great that the cell walls stretch out of proportion to the ability of the cell contents to make new walls. The tissues therefore become thin and imperfectly formed. Such plants are easily killed by dry weather and readily succumb to the attacks of parasitic fungi and other disease-producing agents, which are usually active at just such times. In other words, the conditions least favorable to the growth of the plant or host are as a rule the ones best suited to the rapid development of certain of its parasitic enemies.

From what has been said it is evident that turgidity must depend primarily upon the absorption of water from the soil, and as turgidity is necessary for growth there is an intimate relation between the latter and the absorption of water by the roots. The amount of water necessary to keep the cells at maximum turgidity would be comparatively small if it were not for the fact that evaporation is constantly lowering the quantity. The growth of the plant, therefore, depends largely on whether or not the roots are able to supply the demands made by evaporation from the foliage and at the same time keep the cells in the necessary condition of turgidity.

LOSS OF WATER BY EVAPORATION FROM THE FOLIAGE.

Under ordinary conditions plants lose very large quantities of water by evaporation, it having been shown, for example, that in a dry, hot day a grass plant will lose an amount of water equal to its own weight.

Ordinary meadow grass is about 70 per cent water, and estimating the crop of hay at 2 tons per acre, the weight of the fresh grass, not counting the roots, would be about $6\frac{1}{2}$ tons. This would represent the amount of water evaporated by an acre of grass in a dry, hot day. Hellriegel estimates from many observations that about 310 parts of water pass off by evaporation for every part of dry substance added to a plant. In 2 tons of hay there are 3,808 pounds of dry substance. According to Hellriegel's proportion, therefore, 1 acre of hay would evaporate about 527 tons of water during the season of growth. An average crop of wheat is 720 pounds of grain and 1,500 pounds of straw to the acre; allowing 15 per cent of water in the air-dry material, there would be produced 1,887 pounds of dry material. During its season of growth this crop would evaporate about 261 tons of water. Other crops will lose nearly in the same proportion. One inch of rainfall per acre is equal to about 100 tons of water. The hay crop, therefore, evaporates an amount equal to only about $5\frac{1}{4}$ inches of rainfall, and a wheat crop about $2\frac{3}{8}$. This of course is only an average. In very moist times either crop would lose less in proportion to the amount of dry substance and in very dry times more. In any case, however, it is seen that plants of this class actually evaporate only a small proportion of the water that falls during the growing season.

The problem, therefore, which presents itself is how to make available to the plant more of the water which falls. This may be accomplished in four ways: (1) By methods of cultivation and of fertilization of the soil in order to keep the water from running to waste; (2) decreasing the evaporation from the soil by the same means and possibly also by mulching; (3) decreasing the evaporation from the plants; and (4) by conserving the water and using it in irrigation. The first two lines of investigation and the last belong particularly to the domain of soil physics; the third, while intimately connected with soil physics, belongs more especially to plant physiologists for solution. It may not be out of place, therefore, to point out some of the means by which evaporation from plants may be controlled.

CONTROLLING EVAPORATION.

As already shown, some of our agricultural plants evaporate 310 parts of water for every part of dry substance made. It must not be concluded from this fact, however, that the plants have to evaporate this much water in order to store the normal amount of dry material. On the other hand, it has been demonstrated in practice and by experiment that the amount of dry substance stored and the vigor of the plant is greater in proportion as evaporation is decreased, other conditions remaining the same.

Most of the water evaporated by growing plants is lost, at least in the middle and later stages of growth, through the stomata or breathing pores, situated in the epidermis of the leaves and opening into the

intercellular spaces, as before described and as shown in figure 15. These pores may open and close, under certain conditions, by the contraction or expansion of the guard cells. When the stomata are open, as they usually are in bright light, there is free access of the gases in the air to the starch-manufacturing cells of the leaf. One of the gases (carbon dioxide) taken in this way is the main ingredient of starch and sugar, and in fact furnishes the material which makes up the larger per cent of the dry-weight of the plant. Vegetable physiologists are agreed that the main purpose of the stomata is the admission of this gas and one other, oxygen, to the working cells of the leaf. The air in the intercellular spaces is always saturated with moisture, especially when the leaves are in bright sunlight. When the stomata are open the moisture escapes to the dry outside air, just as it may escape from a moist greenhouse when the ventilators or doors are opened for ventilation. We must have fresh air in the greenhouse, but we can not get it without losing some of the moisture. The rapidity with which the moisture in the greenhouse will pass out depends on the extent to which the ventilators are open, the amount of moisture already in the outside air, and the rapidity with which the air next to the ventilators, and therefore more highly charged with water from the damp air inside, is carried away by the wind. The same conditions hold for the plant. The evaporation, which may be looked upon as a sort of necessary evil, will be less rapid in moist air than in dry air, and will be increased by air currents or wind. If we can increase the amount of moisture in the air we can decrease the evaporation from the plants with which it comes in contact. This suggests the use of trees, especially in sections where hot, dry winds prevail, as a means of breaking the force of the wind and moistening and cooling the air.

Another direction in which we may possibly hope to gain control over loss of water by plants is by increasing the power of the cells of the plant to hold on to the water which they contain, and in this way to resist evaporation more effectively. For many years it has been known through the work of Senebier, Sachs, Burgerstein, Vesque, and others that the presence of various salts and acids in the soil has a marked influence, under certain conditions, on the evaporation of water from the plants whose roots were exposed to the solution of the salts. In some cases the effect was to increase evaporation and absorption, in others to decrease it. The problem needs to be reinvestigated with the practical end in view of increasing absorption and decreasing evaporation. Some late investigators have claimed that the water-holding power of the cells is increased by spraying the leaves with certain solutions, especially Bordeaux mixture. This is certainly true under some conditions, but not so in all cases. It, however, opens up another line in which we may hope to gain some knowledge of the methods of controlling evaporation.

SUMMARY.

The facts presented show—

(1) That water makes up the largest proportion of the weight of green plants, indicating at once its great importance.

(2) That water, with the food which it contains, is obtained by plants exclusively through the roots, and therefore a well-developed root system is essential to the best development of the plant.

(3) That the development of root systems may be controlled in various ways, thereby increasing or decreasing their ability to absorb water and food from the soil.

(4) That a saturated soil is detrimental to the growth of roots; a soil about half saturated is most favorable to their growth and therefore favorable to the growth of the whole plant.

(5) That growth is dependent on the turgidity of the cells, and turgidity is dependent on the absorption of water by the roots.

(6) That the water absorbed by roots is continually being lost by evaporation from the leaves. If the loss is equal to or greater than the absorption, the plants will cease growing, and unless the absorption is increased or the evaporation decreased the plants will die.

(7) That evaporation may be controlled by increasing the amount of moisture in the air, by protection from hot winds, and by the use of certain substances in the soil or on the leaves to enable the plant to hold on to the water that it has.

Finally, then, an accurate knowledge of the relation of water to the growth of plants will enable us to control more fully the development of the plant as a whole, and also the relative growth of its parts. It will show us how to so modify the growth of the plants that they may be able most successfully to withstand adverse conditions and produce the most valuable substance for a given amount of labor.