

ROOT RESISTANCE AS A CAUSE OF DECREASED WATER ABSORPTION BY PLANTS AT LOW TEMPERATURES

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(WITH FIVE FIGURES)

Introduction

It is well known that low soil temperatures decrease the absorption of water by plants. Many years ago SACHS (24) reported that tobacco and gourd plants growing in moist soil under conditions favoring a low rate of transpiration wilted when the soil was cooled to 3° to 5° C., but recovered when the soil was warmed to 12° to 18° C. Cabbage and turnips were less affected, absorbing enough water at a soil temperature just above freezing to prevent wilting during times of moderate transpiration. A few years later VESQUE (29) made further studies using a potometer method in which the roots of *Hedera helix* were immersed in water and cooled to low temperatures. He reported that absorption by transpiring plants decreased as the temperature was decreased although some absorption occurred even at 0.5° C. The most rapid decrease occurred between 15° and 10° C. VESQUE stated that since temperatures higher than 15° C. sometimes resulted in an increase and sometimes in a decrease in absorption, it was impossible to decide as to the real effect.

KOSAROFF (17), by the use of potometers, made an extensive investigation of the effects of low temperature on water intake through living root systems and root systems killed by scalding. He found that lowering the temperature from about 20° C. to freezing retarded the absorption of water by living root systems of *Phaseolus* and *Pisum* 25 or 30 per cent. but did not decrease the absorption of water through dead root systems. Lowered temperature decreased water intake through cut branches of woody plants, but not as much as through living root systems. KOSAROFF also reported that certain species including *Sinapis alba* and *Chrysanthemum indicum* were able to absorb water from soil at -1° C.; *Chrysanthemum indicum* and *Salix* absorbed water from ice in which their roots were frozen. Since the claim that absorption occurred was based on recovery of wilted leaves in a humid atmosphere, it might be supposed that recovery was brought about by movement of water from stem to leaves rather than by absorption through the roots. KOSAROFF discounted this explanation, however, since shoots not in water or ice failed to recover their turgor in a saturated atmosphere.

STAHL (25) reported guttation from the leaves of oats, barley, wheat, and *Geranium pyrenaicum* with roots in soil cooled to approximately 0° C. This, he believed, indicated that some absorption was occurring even at freezing. DUNCAN and COOKE (12) found that the rate of absorption by sugar cane

plants decreased as the water in which their roots were immersed was cooled from 28° to 10° C. They also state that sugar cane plants growing in well watered soil have been observed to wilt upon cooling the soil to about 8° C.

CLEMENTS and MARTIN (7) investigated the effects of soil temperature on the rate of transpiration of *Helianthus annuus*. The rate of transpiration decreased but slightly with decreasing soil temperature from 37° to about 13° C., but decreased rapidly below 13° C., being reduced to one half at about 3° C. The plants begin to wilt at about 4.5° C. and were completely wilted at 1° C., but rapidly recovered when the soil was again warmed. All plants in these experiments were exposed to similar atmospheric conditions.

ARNDT (1) reported that cotton plants exposed to the sun in an unshaded greenhouse wilted at soil temperatures of 17° to 20° C. and plants in solution cultures wilted at 10° to 18° C.

It is probable that, aside from deficient soil moisture, low soil temperature is the most important environmental factor affecting the rate of water absorption. Considerable so-called winter injury, particularly of evergreens, is really injury from desiccation brought about by bright sun and wind which causes excessive transpiration at times when the soil is frozen, or near freezing, so that absorption is too slow to replace the water lost. MICHAELIS (21) has suggested that this is an important factor in determining the tree line in mountains. WHITFIELD (31) and CLEMENTS and MARTIN (7) also believe that the low soil temperatures occurring at high altitude influence plant growth.

TRANSEAU (28) believed that the xeromorphic characteristics of northern bog plants were caused by slow absorption of water resulting from the low temperatures and poor aeration existing in such bogs. Similar anatomical characters could be produced experimentally by growing plants with low soil temperatures, poor aeration, or in dry sandy soil. FIRBAS (13), on the other hand, reported that low temperatures did not interfere with the absorption of water by plants native to German bogs and decided that decreased absorption resulting from low temperatures could not be a cause of their xeric structure. DÖRING (11) studied the effects on absorption of transferring plants in potometers from 20° to 0° C. and found that while the rate was decreased 70 or 80 per cent. in some species it was not decreased at all in other species.

It is not surprising that soil temperature often exerts a marked influence on the rate of water intake since it can affect the process in several different, although more or less related, ways. The more important of the suggested causes for decreased absorption at low temperatures are as follows:

1. Lowering the soil temperature decreases the rate of movement of water from the soil to the absorbing surfaces of the roots. This effect has not been measured directly with root systems, but the writer (19) found the water-supplying capacity of the soil as measured with soil-point cones to be only

one-half to one-third as great at 0° as at 30° C. WILSON (32) also found that the water-supplying capacity was decreased at low soil temperatures. This of course would not be a factor in potometer experiments where the roots are in water. CLEMENTS and MARTIN (7) believed it was of little importance in their experiments on plants rooted in soil, but it seems probable that under certain conditions it may be of some importance.

2. Low temperatures retard the elongation of roots. Since the continual extension of root tips into contact with the water films surrounding hitherto untouched soil particles is very important in making the soil moisture available, a decrease or cessation of root elongation will probably decrease the rate of absorption. This would be most important in soils with a moisture content below the field capacity, a condition which commonly exists in the field.

3. The permeability of cells decreases as the temperature is lowered. DELF (9) found that the rate of plasmolysis and hence permeability of the cell membranes of dandelion scapes and onion leaves decreased with decreasing temperatures from 35° to 5° C. A temperature above 35° seemed to have an injurious effect on permeability as the tissue shrank even in water above this temperature. STILES and JØRGENSEN (27) studied the rate of absorption of water by carrot and potato tissue and found that it decreased with lowering of temperature from 30° to 10° C. According to STILES (26) who has summarized the literature on this subject, permeability to water increases with increasing temperature to at least 30° C., above which the time factor appears. The temperature coefficient for the rate of diffusion through cell membranes was found to be much higher than that for diffusion in aqueous solutions. The causes of the apparent decrease in permeability are at least partly considered in the next two paragraphs.

4. The viscosity of protoplasm and of the colloidal gels in the cell walls is much higher at low temperatures. The increased viscosity probably retards the movement of water across the mass of living cells lying between the soil and the xylem of the roots. WEBER and HOHENEGGER (30) found the viscosity of protoplasm in the root cells of *Phaseolus* seedlings to be about 4 times as great at -2.0° C. and 3 times as great at 5.0° C. as at room temperature. BĚLEHRÁDEK (2) cites other work indicating a general increase in viscosity of protoplasm at low temperatures and suggests that this may slow down diffusion of various substances and cause the high temperature coefficients characteristic of some biological processes. These changes in viscosity are probably concerned in the changes in permeability accompanying changing temperature which were discussed in paragraph 3.

5. The viscosity of water increases as the temperature decreases, being twice as high at 0° as at 25° C. This not only slows down the rate of movement from soil to roots but must considerably decrease the rate of movement through the root cells themselves. It is doubtless an important factor in the low water-supplying capacity of cold soils previously mentioned. The vapor

pressure of water is decreased, falling from 23.75 mm. of mercury at 25° C. to 4.57 mm. at freezing, markedly affecting diffusion and osmotic processes.

6. The physiological activity of the root cells, especially the rate of respiration, is decreased by low temperature. This would be particularly important if the absorption of water is dependent directly or indirectly upon the expenditure of energy by the root cells themselves. HENDERSON (14) found a correlation between the rates of respiration and absorption in roots of corn seedlings and suggested that energy needed for water intake is made available by respiration. HEYL (15) reviewed the literature on root pressure and presented data indicating that exudation phenomena show a marked positive response to increased temperature. This, together with other facts, led him to conclude that root pressure is probably an electro-osmotic phenomenon dependent on the respiratory activity of the root cells as a source of energy. CRAFTS and BROYER (8) have recently advanced an osmotic theory of root pressure which depends on the physiological activity of the cortical cells to maintain a high concentration of solutes in the xylem vessels.

Little definite evidence concerning the relative importance of the various effects of low temperature on water absorption has ever been presented. It seems, however, that in most instances decreased absorption cannot be caused primarily by decreased water-supplying capacity of the soil nor by decreased rate of root extension. Plants with their root systems in well-watered soil and in dilute nutrient solutions or tap water can be caused to wilt in an hour or less by lowering the temperature of the soil or the water to a few degrees above freezing. Root extension and water supplying capacity cannot be limiting factors on absorption under such conditions.

There has been a general tendency to ascribe the reduced absorption of water at low temperatures to decreased physiological activity of the root cells. Decreased temperatures are accompanied by decreased respiration and decreased secretory activity of the living cells, resulting in little or no root pressure at temperatures near freezing. DÖRING (11), for example, found that cooling the root systems of several species to 0° C. stopped bleeding or reduced it to a very low value in only five minutes. It has been found, however, that a decrease in secretory activity is inadequate to explain the decrease in absorption. BOONSTRA (5) observed that the rate of transpiration of peas was greatly decreased by low temperature. He decided, however, that the decrease could not have been caused by cessation of any pumping action of the root cells because he was unable to demonstrate the existence of root pressure in transpiring pea plants even at 25° C. In experiments previously described (18) it was found that sunflower plants grown in a culture solution and placed in potometers filled with tap water at 6° C. wilted badly within a half hour. When the roots were cut off under water the rate of absorption rose to nearly 10 times the previous rate, then fell to a new equilibrium at 2.5 times the rate prior to removal of the roots. The tops of

these plants recovered their turgor within 2 or 3 minutes after removal of their roots and remained un wilted for the duration of the experiments, or more than an hour. These results indicate that the root pressure mechanism was not playing an essential part in absorption; the wilting attendant upon cooling the roots did not result from failure of the roots to "pump" sufficient water into the tops, but from an excessively high resistance to water movement across the tissues into the xylem of the roots themselves. This high resistance must be effective in slowing down water intake regardless of the mechanism involved.

It was suggested by DÖRING (11) that since little or no bleeding occurs at low temperatures most of the decrease in water absorption at these temperatures must result from increased resistance to water movement across the living cells of the roots. It has been shown by the writer (20) that the living cells (probably principally the cortical cells) across which water passes before it can enter the xylem offer considerable resistance to water movement even at ordinary temperatures. This is probably the principal reason for the lag of absorption behind transpiration which seems to be characteristic of plants even when adequately supplied with water. It seems probable that the resistance to water movement would vary with temperature and would be much greater at low temperatures. Probably the best data on this are from an experiment by BODE (4) in which the rate of water movement through sunflower root systems growing in soil and attached to a vacuum pump was found to increase from 10° to 30° C. This seems to indicate that the resistance to water movement through the roots varies with temperature. In view of these facts, an extensive investigation was made of the effect of temperature on the resistance offered by the tissues of the root to water movement.

Methods and results

The sunflower and tomato plants for these experiments were grown in soil in metal containers, or in nutrient solutions, until strong stems and large root systems had developed. This required from four to six weeks. The tops were then removed near the first node and 5 ml. pipettes graduated in 0.05 ml. were attached to the stumps by rubber tubing and sealed with a mixture of paraffin, beeswax, and tallow. Enough water was added to each pipette to bring the meniscus up to the graduations on the pipette and vacuum was applied for a few seconds to remove any air bubbles.

The root systems, in their containers, were then placed in a water bath which could be maintained at any temperature from freezing to 50° C. by refrigerating and heating units. The pipettes were attached to a vacuum pump by rubber tubing and T-tubes and the pressure on the cut stems was reduced to a point where a pressure gradient of 64 cm. of mercury existed from exterior to interior of the root system. This pressure gradient was

maintained for periods of 30 minutes or one hour, depending upon the rate of absorption. By reading the pipettes at the beginning and end of the period the amount of water absorbed was accurately determined. In certain experiments similar groups of plants were prepared, but not attached to the vacuum pump. The rate of exudation at various temperatures was determined from these plants. The results given are averages of determinations on at least six plants.

In the earlier experiments a single group of plants was used for determinations over the entire range of temperatures from near freezing to as high as 40° C. It was suggested that perhaps a longer period of adjustment to a new temperature was needed than was permitted by this method and that the effects of previous exposure to low temperature might affect the behavior at high temperatures. Several experiments were then performed in which the absorption of a group of six sunflower plants was first determined at 25° C. and then at one of the experimental temperatures. These plants were then discarded and the absorption of a second group was determined at 25° C. and at some other experimental temperature. This procedure was repeated for each temperature at which determinations were to

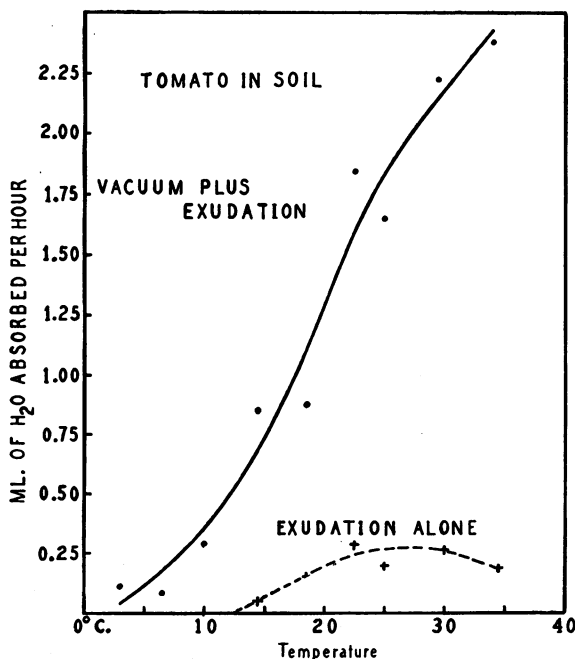


FIG. 1. Water movement in various temperatures through living tomato root systems growing in soil. Each point represents the average of six determinations. The determinations at various temperatures were made on the same plants. The upper curve is for a group of plants attached to a vacuum pump, while the lower curve shows exudation alone.

be made. Thus any one group of plants was exposed to only two temperatures; 25° C., which was approximately that at which it had been grown, and one other temperature which was higher or lower. The rates were then plotted as percentages of the rate at 25° C. The results thus obtained were similar to those obtained when one group was observed at several temperatures. The results of various experiments are much more easily compared, however, when calculated as percentages of the rate at 25° because differences caused by variations in size of root systems are eliminated. The results are shown graphically in figures 1, 2, and 3.

Figure 1 shows the behavior of tomato plants growing in soil at approximately field capacity. It will be noted that the maximum rate of exudation occurred at 22.5° C. and that the rate tended to decrease above this temperature and exudation ceased or became too slow to measure at about 12° C. The highest rate of exudation was only about 15 per cent. of the rate at the same temperature for similar plants attached to a vacuum pump. The rate of water movement at 5° C. through the roots attached to a vacuum pump was only 6 per cent. of the rate of 25° C. Increasing the temperature to 34° C. increased the rate of water movement to 143 per cent. of the rate at 25° C. In a similar experiment with sunflowers the maximum rate of exudation of plants not attached to a vacuum pump occurred at 25° C. and exudation became negligible at about 2.5° C. The highest rate of exudation was only about 17 per cent. of the rate at the same temperature for plants attached to a vacuum pump. BODE (4) also found the maximum rate of exudation of sunflowers at about 25° C. The rate of exudation is quite variable in individual plants, however, and the maximum rate of exudation is sometimes at 35° or 40° C. or higher.

Figure 2 shows the rate of water movement at various temperatures through living sunflower root systems in soil and in water, and through dead root systems in water. All of these root systems were attached to a vacuum pump and maintained under a pressure gradient of 64 cm. of mercury. It will be noted from the graph that the effect of temperature on the rate of water movement through living root systems in moist soil and in water was essentially the same. This perhaps indicates that roots can absorb water as readily from soil near the field capacity as from liquid water. In both instances the rate of movement was much decreased by lowering the temperature. The rate of movement through dead roots was less affected by temperature, indicating that the resistance to flow does not increase as much with lowered temperature in dead roots as in living roots. The lower curve indicates the decreasing viscosity of water with rising temperature plotted as percentages of the reciprocal of the specific viscosity at 25° C. It will be noted that the slope of this curve is approximately the same as that for the rate of water movement through the root systems. The viscosity of water

is about twice as great at 0° C. as at 25° C. and the rate of water movement through the dead roots at 1° C. is about half of the rate at 25° C. This seems to indicate that the viscosity of water may be the principal factor limiting the movement of water through the dead roots. Some additional factor must exist in the living roots which causes their permeability, and hence their resistance to water movement, to change much more with changing temperature than does the resistance to water movement of the dead roots. This additional factor probably is the change in viscosity of the protoplasm and of the colloidal gels of the cell walls. WEBER and HOHENEGGER (30) state that the

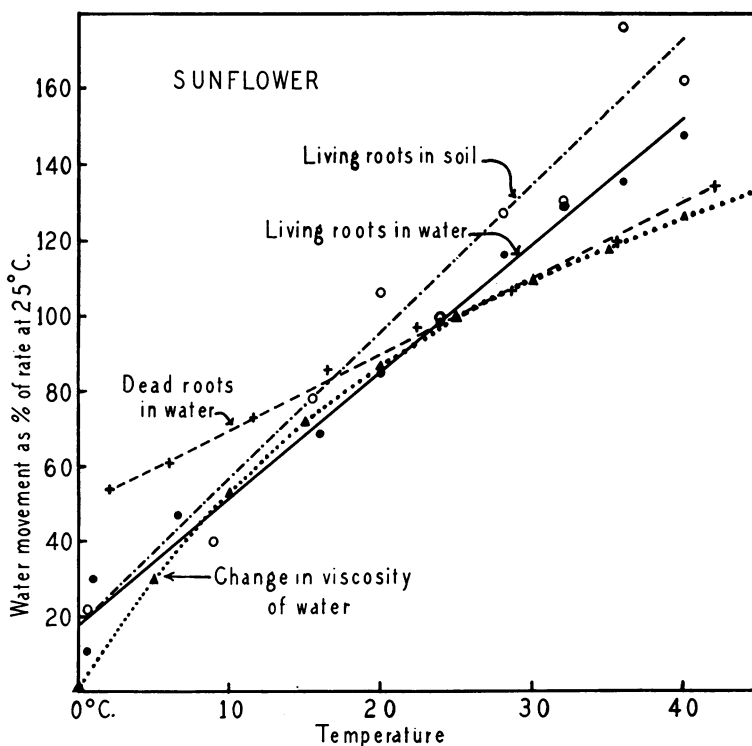


FIG. 2. Water movement through sunflower root systems attached to a vacuum pump. Plants were under vacuum for one hour and a different set of six plants was used for each temperature in all determinations on living roots. The curve for viscosity is the reciprocal of the actual viscosity, plotted as percentages of the value at 25° C. All rates in figures 3 and 4 are plotted as percentages of the rate at 25° C.

viscosity of the protoplasm of *Phaseolus epicotyls* is about 3 times as great at 5° C. and about 4 times as great at -2.0° C. as at 19° to 22° C. The greater increase in viscosity of protoplasm as compared with that of water probably explains the greater decrease in water movement through living root systems. Killing the cells results in collapse of the protoplasts and dis-

organization of the strands of cytoplasm passing through the cell walls, thus lessening the resistance to flow.

The results of these experiments are similar to those of BODE (4) who measured the rate of water movement at various temperatures from 10° to 30° C. through sunflower root systems attached to a vacuum pump. All the data available indicate a much greater reduction in water movement at low temperatures than the 25 or 30 per cent. reported by KOSAROFF (17). Some variations occur between different groups of plants of the same species, perhaps because of differences in heredity, past treatment, and age. Differences between species might also be expected, but the behavior of sunflower, tomato and privet was essentially the same in these experiments. It would be expected that cotton root systems which, according to ARNDT (1), may wilt at a soil temperature of 15° or 18° C. would show greater reduction of water movement in that temperature range than do sunflowers.

That the resistance to water movement lies chiefly in the protoplasm is indicated by the fact that much more water will pass through a dead root system than passed through the same root system under the same conditions of time, temperature, and pressure while it was alive. The rate of water movement at 25° C. through dead sunflower root systems immersed in water was 3.5 to 6 times the rate through the same root systems while alive. At 1° C. the rate was 5 to 10 times the rate through living root systems. RENNERT (23) reported that root resistance was greatly decreased by killing the roots, and the writer (18) has previously reported large increases in water movement after killing the roots.

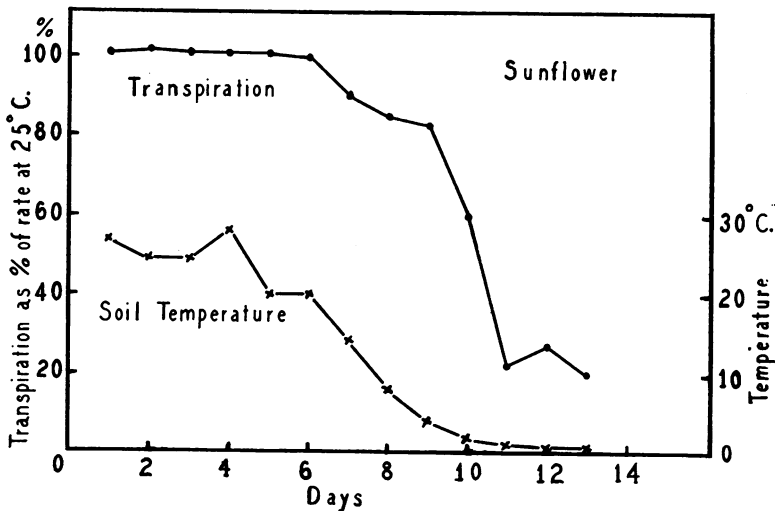


FIG. 3. Effect on transpiration of sunflowers of slowly cooling the soil. Rate of transpiration is plotted as percentages of rate of control group kept in adjacent water bath with soil temperatures of 25° C.

Figure 3 shows the decrease in rate of transpiration of a group of sunflower plants growing in soil which was slowly cooled. This was accomplished by immersing the cans of soil in which the roots were growing in a water bath which was cooled about 4 degrees daily by a refrigeration system. The rate of transpiration is given as percentages of the rate of a group of similar control plants in an adjacent tank kept at about 25° C. The light intensity and air temperatures were essentially the same for the tops of the two groups. It will be noted that at 1° C. the transpiration rate of the sunflowers fell to 20 or 25 per cent. of the rate of the controls at 25° C. This reduction agrees rather closely with the reduction in rate of water movement obtained with root systems attached to vacuum pumps as shown in figure 2. This agreement in results tends to strengthen the belief that data obtained by attaching a vacuum pump to the root system are indicative of what is occurring in the root systems of intact transpiring plants of the same species. A similar experiment was performed on potted plants of privet (*Ligustrum japonicum*). After the soil containing the root systems of these plants had been slowly cooled to about 1° C. the rate of transpiration was about 30 per cent. of the rate of the controls at 25° C.

Discussion

In considering the factors affecting the absorption of water it should be remembered that there appear to be two types of absorption occurring in many plants. These two types of absorption apparently may occur either simultaneously or independently, and their relative importance probably depends on the rate of transpiration and the internal water economy of the plant. RENNER (22) has differentiated these two types as "active" and "passive" absorption, but the writer prefers to term them "physiological" and "physical" absorption.

Active or physiological absorption is some sort of osmotic or secretory process, the mechanism of which cannot be explained fully at present. It is dependent on the presence of living cells in the roots and is responsible for root pressure and exudation from cut stems. Passive or physical absorption is a movement of water across the cortex along a gradient of decreasing vapor pressure from soil to xylem. This pressure gradient results from the decreased pressure or tension on the water conducting system which usually exists in transpiring plants. In these experiments the conditions bringing about physical absorption were partially simulated by attaching the root systems to a vacuum pump.

Previous experiments (20) have shown that at 25° C. there is considerable resistance to the movement of water across the mass of living cells lying between the epidermis and the xylem. The results of the present experiments are believed to indicate that the principal reason for the wilting of

plants whose roots are in cold soil is the reduction in physical or passive absorption caused by increased resistance to water movement across the tissues of the roots. Decreasing the temperature increases the viscosity of water, and to an even greater extent increases the viscosity of the protoplasmic membranes through which the water must pass. As a result of the increased friction less water moves into the roots with a given pressure gradient. The writer prefers to speak of the decreased water movement as being caused by changes in "root resistance" rather than by changes in permeability. Permeability is usually considered with respect to individual membranes. The intake of water is affected not only by changes in the permeability of all the membranes through which the water must pass, but also by changes in the physical properties of the water itself, and the total effect can best be described as root resistance.

The minor part in water intake played by physiological absorption and root pressure phenomena is evident when one observes that the amount of water exuding from cut stems is usually less than 20 per cent. of the amount obtained under a pressure gradient of only 64 cm. of mercury. Such a comparison is open to the criticism that removal of the top decreases the activity of the roots and hence decreases the quantity of exudation and exudation pressure. This effect is probably unimportant during at least the first two or three hours after decapitation as the rate of exudation usually does not begin to decrease for several hours. The resistance of the cortical cells is equally important regardless of whether water is being secreted into the xylem by some root pressure mechanism or moves by mass flow along a gradient of decreasing pressure caused by transpiration.

It appears that WILSON (32) is correct in stating that the importance of changes in the viscosity of water have been under-emphasized. STILES (26) points out that the temperature coefficients obtained for movement of water into various living plant tissues are considerably higher than the temperature coefficient for a physical process such as diffusion of a solute into water. DENNY (10) found the temperature coefficient for the passage of water through non-living seed coats to be higher at a low than at a high temperature. It was also higher than the temperature coefficient for pure diffusion. It is not surprising that the temperature coefficients for movement through such tissues and membranes do not agree with those for diffusion of solutes in water, since the conditions are much more complex in the experiments with plant membranes. The viscosity of the water, the protoplasm, and other colloidal materials of the tissues themselves are increased by lowering the temperature. All of these changes increase the friction or resistance to flow through the membranes and the combined effects will be considerably larger than for diffusion of a solute in water.

According to data of BIGELOW (3) the rate of movement of water through porcelain and collodion membranes at various temperatures is closely related

to the viscosity of water. In a strict sense the permeability of a porcelain membrane is probably unaffected by small changes in temperature and any change in rate of flow of water is the result of changes in physical properties of the water itself. To discuss the effects of temperature on the permeability of non-living seed coats, porcelain membranes, or dead roots probably misplaces the emphasis. Perhaps, however, we can speak of "membrane resistance" in such instances.

The effects of temperature on the rate of movement of water through various types of non-living membranes is shown in figure 4. The rates of

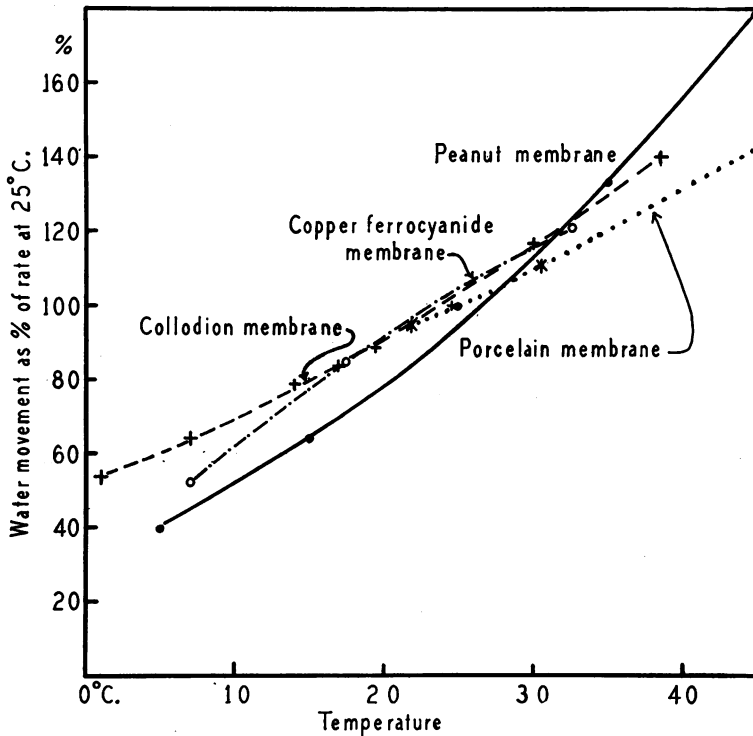


FIG. 4. Effect of temperature on rate of water movement through various types of non-living membranes.

movement are all plotted as percentages of the rates at 25° C. in order to facilitate comparison with the rates of water movement through living and dead root systems plotted in figure 2. The data for peanut seed coats are from DENNY (11). The data for the porcelain and collodion membranes are from BIGELOW (3) and are the rates of flow of water under constant hydrostatic pressure at various temperatures.

Comparison of figures 2 and 4 show that the lines for water movement by both pressure and diffusion through the mechanical membranes have the

same slope as the line for water movement under pressure through dead root systems. The line for movement by diffusion through the peanut seed coat rises somewhat more rapidly with increasing temperature and has a slope similar to that for water movement through the living root systems.

As shown in figure 2, the slopes of these lines resemble the slope of the curve for decreasing viscosity of water with increasing temperature. If viscosity of water were the only factor affecting the rate of movement of water through the membranes at the various temperatures, the lines for rate of movement should be somewhat curved to conform to the curve for the viscosity of water. It is possible that the surprisingly straight lines observed when these diverse data are plotted result from a balancing interaction between the changes in vapor pressure and viscosity that accompany changes in temperatures. Figure 5 shows the vapor pressure of water plotted as percentages of the vapor pressure at 25° C. and the curve for the recip-

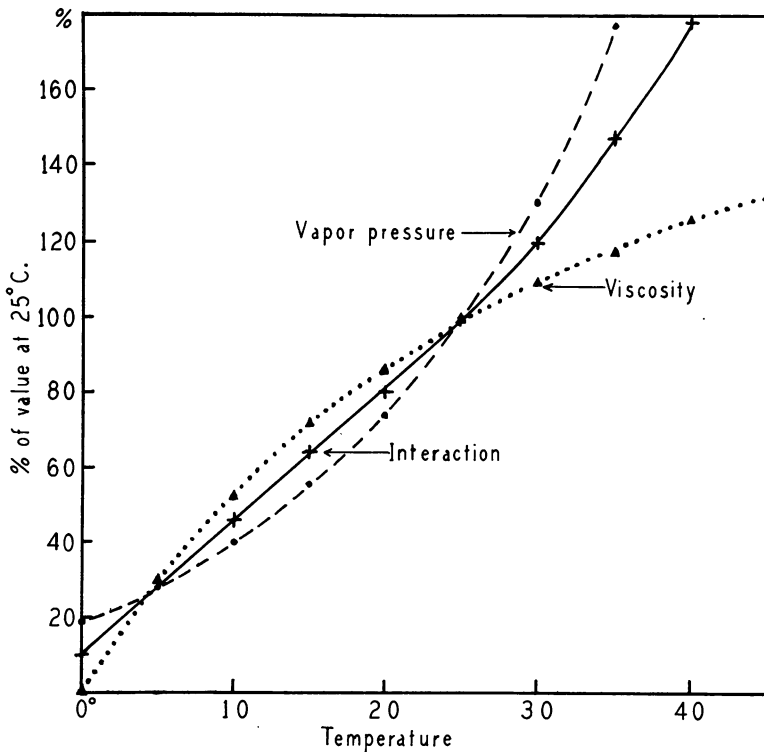


FIG. 5. Changes in viscosity and vapor pressure of water plotted as percentages of values at 25° C. The solid line is drawn equidistant between the two curves showing their possible interaction on water movement.

rocal of the viscosity plotted in the same manner. It will be observed that the line connecting points which are equidistant between the two curves is

practically straight, up to 30° C. Above 30° C. it curves upward because the increase in vapor pressure begins to occur more rapidly than the decrease in viscosity. This suggests that the straight lines obtained for the movement of water are the results of the balancing interaction of viscosity and vapor pressure. The line for water movement by diffusion through peanut seed coats definitely curves upward, especially at 35° and 45° C., as would be expected in a pure diffusion process dependent on a vapor pressure or activity gradient.

Changes in viscosity of water and especially in the viscosity of the protoplasm possibly have some effects on the absorption of minerals. HOAGLAND and BROYER (16) report a Q_{10} for salt accumulation by roots of 2.5 to 5.0. No doubt this results largely from the fact that salt accumulation depends on the metabolic activity of the cells. It is likely, however, that if resistance to water movement is four or five times as great at temperatures near freezing as it is at 25° C., then resistance to the movement of ions into cells is also increased by lowered temperature.

While the effects on plant growth of decreased water absorption caused by low soil temperatures have been studied frequently by ecologists and physiologists they possibly have not been considered adequately by agronomists, horticulturists, and others working on problems of plant production. According to investigations previously cited (1, 12), it appears that the absorption of water by cotton and sugar cane plants is checked at temperatures which are not low enough to cause wilting in sunflower or privet plants. BROWN (6) has recently published an interesting study of the effects of soil temperature on the growth of Bermuda grass, and Kentucky and Canada bluegrass. When the soil temperature was 21° C. and the air temperature 38° C. the leaves of Bermuda grass wilted, apparently because of inadequate absorption of water; the other two species did not wilt. Absorption of water by Bermuda grass was definitely retarded at soil temperatures of 4.4° and 10° C. while the other two species showed no wilting. It seems possible that the growth of such plants as cotton and Bermuda grass might be hindered by moderately low soil temperatures even though the air temperatures are entirely favorable for growth. One would expect this to be characteristic of most southern species but it is probably unsafe to generalize on this matter. DÖRING (10) studied the effect of low temperatures on the water absorption of 57 species having quite different climatic and temperature requirements; he found no consistent relationship between habitat and the extent to which low temperatures checked absorption. The data on cotton and Bermuda grass, however, indicate the possibility that the effects of low soil temperatures on the absorption of water and minerals might limit the growth of plants as effectively as low air temperatures.

Summary

1. The rates of water movement through root systems of tomato and sunflower attached to a vacuum pump were measured at constant pressure over a temperature range from 0° to 40° C. It was found in all experiments that the rate decreased with lower temperatures, both for plants in soil and in water. The rate of movement through sunflower roots at temperatures slightly above freezing averaged about 20 per cent. of the rate through the same roots at 25° C. and the rate at 40° C. averaged about 160 per cent. of the rate at 25° C.

2. The rate of exudation from root systems not attached to a vacuum pump was highest at about 25° C., decreasing with both increased and decreased temperature. The rate became too low to measure at about 12° C. in tomatoes and 2.5° C. in sunflowers. The highest rate of exudation was less than 20 per cent. of the rate obtained with the same or similar plants attached to a vacuum pump under a pressure gradient of 64 cm. of mercury.

3. The rate of movement of water through dead sunflower roots attached to a vacuum pump also decreased with decreasing temperature, but not to the same extent as in living roots. The rate at 0° C. was about 50 per cent. of the rate at 25° C. and the rate at 40° C. was 130 per cent. of the rate at 25° C.

4. It is believed that the decreased rate of movement of water through dead roots at low temperatures is largely caused by the increased viscosity of water itself. In living roots the added effects of decreased permeability, probably resulting from increased viscosity of the protoplasm and of the colloidal gels of the cell walls, causes an even greater resistance to water movement. The resistance to water movement through living roots of sunflower appears to be four or five times as great at temperatures near freezing as at 25° C. At 40° C. the resistance is only a little over half that at 25° C.

5. The principal cause of decreased water absorption by plants at low temperatures appears to be the combined effects of decreased permeability of the root membranes and increased viscosity of water, resulting in increased resistance to water movement across the living cells of the roots. The effects of low temperature in decreasing root extension, root respiration, active absorption and root pressure phenomena are of secondary importance. The increase in root resistance with decreasing temperature probably is effective, however, in slowing down physiological, or active, absorption of water, and possibly the absorption of solutes by roots.

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