WATER ABSORPTION IN THE COTTON PLANT AS AFFECTED BY SOIL AND WATER TEMPERATURES[1]

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Introduction

In experiments at the South Carolina Experiment Station with solution cultures of cotton (*Gossypium hirsutum* L.) it was occasionally noted in early spring that severe wilting occurred in the morning when the greenhouse temperature had fallen as low as 16° C. during the preceding night. This unusual wilting was apparently due to sunlight causing a rapid rise in air temperature when the solution temperature was low; for the plants recovered quickly when the air temperature was lowered by ventilation until the solutions had become warmed to about 20° C. Similar morning wilting was observed in plants growing in soil when soil temperature was much lower than a rapidly rising air temperature. Because the relation of root absorption to soil temperature is of great importance in the study of plant-water relations and also because the soil and solution temperatures which led to the wiltings just mentioned are higher than those reported for other plants, a study was undertaken to obtain information concerning the relation of root temperature to wilting in the cotton plant under otherwise favorable conditions for its healthy functioning. Some results of that study are briefly set forth in this paper, in the preparation of which the author has been aided by Professor BURTON E. LIVINGSTON of the Johns Hopkins University.

Materials and methods

Observations were made on plants growing in solution and soil cultures. In the latter, young, vigorous, six-week-old plants were used; these had been grown in sheet-metal cylinders (25 cm. in diameter and 30 cm. deep), containing 18 kg. of a fertile sandy-loam soil. The average water content of the soil was held at 60 per cent. of the water-holding capacity, the water loss being replaced semi-weekly. To cool the soil, the cylinders were set in a tank of colder water, the water surface being about 3 cm. above the level of the free soil surface. The water temperature was maintained at approximately 1° below the desired soil temperature by means of an electric automatic water heater and a manually controlled stream of cold water from a refrigerating machine. When the desired soil temperature had been reached, the water bath was raised to that temperature. When lowering of soil temperature was not over 10°, approximately uniform soil tempera-

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tures could be established throughout the soil mass in 5 hours. The soil temperature was measured at a depth of 4 cm. in the axis of the cylinder; if the temperature of parts of the root system differed from this, it was undoubtedly always slightly lower rather than higher, and the total difference was never more than one or two degrees.

In the solution-culture studies, 8-week-old plants, averaging 60 cm. in height, were used. These were well branched and leafy, with numerous floral buds and even young bolls. Two-liter Erlenmeyer flasks were used as containers, a single plant in each. The solution employed, which had been found quite satisfactory for the cotton plant, had the following composition: KNO_3, $0.0014M$; $Ca(NO_3)_2$, $0.0028M$; KH_2PO_4, $0.0007M$; and $MgSO_4$, $0.001M$; ferric citrate, $0.00001M$; $MnSO_4$ and $Na_2B_4O_7$, each $0.00002M$; and $CuSO_4$, $0.0000005M$. The solutions were renewed semi-weekly, water being added as needed to maintain a solution volume of 2 liters. To prevent excessive heating of the solutions by sunlight, each flask was placed in a 9-liter stone-ware jar, with excelsior packing, both jar and flask being covered with a cone of thick paper with a central opening for the plant. During the growth period the solution temperature showed a daily range of approximately 20°–35°. The solution temperature was lowered by a procedure similar to that employed for the soil cultures. During the cooling, heat transfer was accelerated by slowly bubbling air through the solution and by an occasional shaking. In other experiments cooling was accelerated by replacing the solution with a fresh one at the desired temperature before placing the flask in the water bath.

When roots were to be heated, a large cylindrical water bath was brought to the desired temperature before the plant container was suspended in it. This temperature was maintained throughout the experiment by means of a manually controlled electric heater. The container fitted closely into the cover of the bath and a large circular sheet of cardboard was fitted closely around the base of the plant, to prevent heated air from rising around the plant.

Air temperature and humidity were recorded by means of a shaded hygrothermograph adjacent to the plants on which the observations were being made.

Experimentation

Unless otherwise noted, all experiments here described were performed in full sunlight in an unshaded greenhouse between April 1 and August 25, 1933. Wilting of the plants first became evident as a loss of turgidity of the leaves and a drooping of their margins. At a more advanced stage (recorded as severe wilting) there was noticeable drooping of the petioles and ends of the branches. During the heat-treatments the areas between the veins usually became noticeably bleached. These bleached areas disappeared on cooling the roots, only to reappear several days later as yellow to brown areas. Such affected leaves usually dropped from the plant within a week.

WILTING INDUCED BY SUDDEN LOWERING OF SOLUTION TEMPERATURE

In twelve tests in which the temperature of the root system was suddenly lowered by replacing the old solution with a new and colder one, the latter being from 10° to 23° colder than the former, wilting began within 20 to 75 minutes. The length of this period showed no consistent relation to (a) the solution temperature at which wilting occurred (which varied from 11° to 16°), to (b) the initial solution temperature (which varied from 28° to 36°), to (c) the temperature lowering to which the roots were subjected (which varied from 10° to 23°), to (d) the current air temperature (which varied from 32° to 36°), to (e) the difference between root and current air temperature (which varied from 17° to 24°), or to (f) the current relative humidity (which varied from 25 to 50 per cent.). The following examples illustrate the actual results of specific experiments:

(1) Solution temperature lowered from 28° to 14°; wilting observed in 20 min., at air temperature 38°, relative humidity 35 per cent.; solution was then allowed to become warmer and plant had fully recovered in 85 min., solution temperature then being 22°.

(2) Solution temperature lowered from 33° to 11°; wilting observed in 17 min., at air temperature 35°, relative humidity 45 per cent.; leaves flaccid and petioles drooped after additional 15 min.; plant fully recovered 3 hr. after removal from the cold bath when solution temperature had risen to 25°.

(3) Solution temperature lowered from 30° to 15°; wilting observed in 45 min., at air temperature 34°, relative humidity 50 per cent.; solution then allowed to become warmer, plant fully recovered in 45 min., when solution temperature had risen to 22.5°.

WILTING INDUCED BY GRADUAL LOWERING OF SOLUTION TEMPERATURE

When the temperature of the roots was lowered gradually by immersing the flask in the cold bath without changing the solution, the processes leading to wilting went on concurrently with cooling, which was usually still in progress when wilting was first observed; at this time record was made of solution temperature and of the time elapsed since cooling began (which is here the same as the wilting time). In eleven tests in which initial solution temperature varied from 20° to 32° and time of cooling varied from 30 to 120 min. (with air temperature ranging from 30° to 39° and relative humidity from 20 to 50 per cent.), the plants wilted at various temperatures between 10° and 18.5°. There were no apparent relations among: (a) temperature difference between solution and air at time of wilting, (b) extent of cooling, and (c) wilting temperature; but larger solution-air differences generally corresponded to more extensive cooling and to lower wilting temperatures. Conversely, none of the three variables just mentioned showed any consistent relation either to (d) wilting (cooling) time or to (e) rate of cooling, but the latter (d and e) were clearly related to each other; *i.e.,* when the rate of cooling was rapid the wilting time was short, and conversely, as might be expected. It may be said in general that, within the frame of these experiments, wilting began at solution temperatures between 10° and 18.5° and that it occurred more promptly when root temperature was lowered rapidly than when cooling was more gradual. The following detailed accounts are representative of the tests with gradually cooled solutions:

(1) Initial solution temperature 21°; wilting began after 30 min., at solution temperature 16.5°; air temperature 32° and relative humidity 35 per cent. at the beginning of visible wilting.

(2) Initial solution temperature 21°; solution cooled for 105 min., when wilting began, at solution temperature 15.5°; air temperature at beginning of visible wilting 35°, relative humidity 25 per cent.

(3) Initial solution temperature 30°; solution cooled for 30 min., when wilting began (11:15 A.M.), at solution temperature 18.5°; air temperature at beginning of wilting 38°, relative humidity 20 per cent. Solution was then allowed to warm to air temperature and recovery was complete before 2:45 P.M., when air temperature was 29.5°; solution was then cooled until it reached a temperature of 11.5°, after 110 min. (4:35 P.M.) but plant did not wilt; air temperature at this time 35°, relative humidity 40 per cent.; sky had been overcast since 2 P.M. Failure to wilt at this low solution temperature was apparently related to cloudiness (see below, effect of shading soil cultures at low soil temperature), decreased air temperature, and increased relative humidity.

(4) Initial solution temperature 25°; solution cooled for 40 min., when wilting began, at solution temperature 10°; air temperature at this time 35°, relative humidity 50 per cent. Solution was then held at 10° for 4 hours longer, at the end of which period (late afternoon) all leaves were flaccid and petioles and ends of branches drooped. Plant regained turgidity the following night with solution at the temperature of the greenhouse, but on the following morning some of the younger leaves were observed to be slightly blackened on their margins. Several days later areas between the veins of these same leaves and of some of the other young leaves, which had not yet reached their full size, became somewhat yellowish and remained so for several days. Subsequent growth was apparently normal, excepting that many young roots had been injured. These had lost their geotropic sensitiveness and elongated at right angles to the pull of gravity; they became somewhat hooked at the ends and each showed a marked constriction behind the tip. The injured roots elongated only slightly, but many healthy branches developed from their older portions.

Wilting induced by lowering of soil temperatures

In studying the influence of unusually low soil temperatures on infection of cotton seedlings, wilting of healthy plants had been observed on clear days with high greenhouse temperature and low relative humidity at times when soil temperature was about 18° or lower. The soil temperature at which such wilting occurred was apparently always essentially the same whether the plants had been grown at constant soil temperatures (18°, 21°, 24°, 27°, 30°), or had been subjected to the daily temperature fluctuations of the greenhouse, or had been subjected to artificially controlled semi-daily temperature alternations (30° by day and 16° by night); also whether the holard at the time of wilting represented 80 per cent. of the water-holding capacity of the soil, or only 60 per cent. This wilting was observed, however, only in full sunlight; it was never observed on cloudy days, even when soil temperature was below 18° and air temperature was relatively high. Furthermore, plants that had wilted in this way on clear days regularly exhibited rapid recovery in the late afternoon when the intensity of solar radiation was rapidly diminishing.

Some special experiments were carried out concerning the effect of shading on the occurrence of wilting. Plants grown in the usual soil containers were arranged in pairs in the same cold water bath; one of each pair was left in full sunlight, while the other was shaded from direct sunlight by a 60-cm. square of thick cardboard supported horizontally 20 cm. above the plant, so that air circulation around the plant would not be greatly modified. These tests were made on clear days in July. The unshaded plants wilted more or less promptly at a soil temperature of 18°, but none of the shaded plants wilted. It therefore appears that intense sunshine and low soil temperature acted in conjunction to produce wilting. The following accounts are representative of these tests with shaded and unshaded plants.

(1) At 8:30 A.M. on July 23 a pair of similar plants were placed in the cold water bath (temperature 16°), where they remained until late in the afternoon of the next day. At 12:15 P.M. the unshaded plant was very noticeably wilted but the shaded one showed no wilting. Soil temperature was then 18° in the central axis, 16° at the margin, air temperature was 36° and relative humidity was 45 per cent. At 3:00 P.M. (air temperature 37°, relative humidity 35 per cent., soil temperature as above) the shaded plant was still unwilted but wilting of the unshaded plant was more pronounced than at 12:15 P.M. (At this time it was observed that similar cultures on a nearby greenhouse bench—unshaded and with soil temperature 41°—showed no wilting.) During the night the wilted plant recovered and appeared perfectly healthy at 8:30 A.M. the following morning, when soil temperature in the central axis was 17°, air temperature and relative humidity being 30° and 60 per cent. The leaves of the unshaded plant became gradually more

flaccid until 2:30 P.M., when the shade was removed. At that time (air temperature 36°, relative humidity 35 per cent.) the shaded plant remained apparently unaffected. At 4:45 P.M. both plants were severely wilted.

(2) July 7, 2:15 P.M., cultures with soil temperature 32° were placed in water baths at 18°, 20°, 22°, and 29°. At 5:00 P.M. (air temperature 38°, relative humidity 20 per cent.), when the soil masses had reached approximately the same temperatures as the baths, the plants in the 22° and the 29° baths were unwilted; those in the 20° bath (soil 22°) were slightly wilted; while those in the 18° bath (soil 20°) were badly wilted. At 8:30 A.M. the following day (air temperature 25°, relative humidity 55 per cent.), none of these plants was wilted, although the soil in the 18° bath had been cooled to 15° by cutting off the electric heater and increasing the supply of cold water. Because of inadequate cold-water supply, the temperature of that bath rose slowly and at 11:00 A.M. the soil had reached a temperature of 18° and the plants were slightly wilted (air temperature 33°, relative humidity 25 per cent.). At 3:00 P.M. these same plants were severely wilted (petioles drooping, youngest leaves more wilted than old ones), although the soil had reached a temperature of 20° at a depth of 4 cm. in central axis (air temperature 39°, relative humidity 15 per cent.). The plants in the 22° soil were unwilted. All wilted plants recovered quickly after sunset, even in the coldest bath, in which the soil temperature had again fallen to 18°.

(3) July 16, 10:00 A.M., six cultures were placed in water bath at 20°; at 2:00 P.M., with soil temperature approximately like that of bath, all plants were unwilted (air temperature 36°, relative humidity 20 per cent.). Three of these plants were then removed to a 17° bath. At 4:20 P.M. (air temperature 37°, relative humidity 20 per cent.) all plants in the 17° bath (soil 18°) were severely wilted, but those in the 20° bath (soil 20°) still showed no signs of wilting.

(4) July 15, 10:00 A.M., several cultures with soil temperature 22° were placed in bath at 16°. At 10:40 A.M. plants were severely wilted (soil temperature at 4 cm. depth 16° in center and 19° near margin; air temperature 32°, relative humidity 28 per cent.). Cultures were then removed to greenhouse bench and plants had completely recovered 35 min. later, at which time soil temperature near margin of cylinder had risen to 20° (air temperature and relative humidity approximately the same as at 10:40 A.M.).

In full sunlight, with low relative humidity and air temperature 30° to 40°, the plants generally wilted at soil temperatures from 16° to 20°, the higher soil temperatures being generally associated with the higher air temperatures and lower humidities. Thus the plants growing in soil wilted at slightly higher temperatures than those growing in solution cultures.

Wilting and other injuries induced by raising solution temperature to 60° C. or higher

Several earlier studies, which have been reviewed by Kramer (**12**), and to which he has added confirmatory observations on cotton and several other plants, have shown that plants, whose roots have been killed by high temperatures, may remain unwilted for several days. Some of the writer's results from experiments with heated roots are in essential agreement with the earlier observations, but some additional effects of the temporary application of high temperature to cotton roots are to be noted.

In routine solution cultures of cotton grown in the greenhouse, the solution temperature frequently reached 40° and remained so for several hours on bright sunny days with no apparent injury to either tops or roots. In special experiments, heating the solution for 75 min. at 50° produced no noticeable injury and no reduction in the rate of transpiration. Prompt wilting and subsequent additional symptoms of injury were produced, however, when the solution around the roots was heated to 70° during a 75-min. period and then held at that temperature for 15 min. For the first day after this treatment, a plant thus treated transpired at about the same rate as the unheated controls; but for the second day and the five succeeding days, its daily transpiration rates were respectively only 14, 31, 38, 19, 23, and 14 per cent. of the corresponding control rates. The effect of this heat treatment on transpiration was thus not immediate, but it became evident after 24 hours. The actual water loss after treatment, however, was considerable, being (for the 7 days in order) 115, 30, 60, 110, 50, 50, and 30 gm. On the last day of this record the transpiration for the control plant was 220 gm., or about seven times as great as that of the heated plant. Similar results were secured with respect to transpiration when the solutions were heated to 60°, except that the retardation of transpiration was more gradual and longer delayed; *e.g.*, a plant whose solution had been heated to 60° in 30 min. and kept at that temperature for 75 min. gave the following successive rates of water loss (expressed as percentages of the corresponding control rates) : 95, 93, 37, 24, 19, 14 gm. Thus notable retardation was not noticeable until the third day, after which it became gradually more pronounced until both the 60°- and 70°-treated plants showed the same degree of retardation. These observations suggest that, although these heat treatments killed or greatly injured the roots, the latter were able to supply water to the rest of the plant at an adequate rate for a day or more after the treatment—the length of this period being shorter with the more severe treatment.

Additional symptoms of injury that accompanied or followed these heat treatments were readily observed. When the solutions were heated to 60° or higher, numerous gas bubbles escaped from the root lenticels while heating was in process, apparently because of gas expansion in intercellular spaces. Also, wilting of the older leaves occurred while the 70° treatment was in progress, but wilting did not occur with the 60° treatments. The 70°-treated plants recovered from wilting during the night and were apparently healthy the following day. Concurrently, however, with the reduction of transpiration on the second day after treatment, wilting of the older leaves again became apparent, areas between the veins became discolored, and there was no subsequent recovery. All plants subjected to solution temperature of 60°, or higher, for a period of 60 min. showed conspicuous light-colored areas between the veins of the older leaves before the end of the heating period. After the solution or soil had cooled to air temperature these areas disappeared, but they reappeared a day or two later as conspicuous yellow or yellow-brown areas. Leaves so affected became abnormally rigid and leathery, never recovered, and eventually fell from the plant. The larger veins of the leaves of the 60°-treated plants retained their bright green color for several days after the discoloration of neighboring areas. Before a leaf dropped these veins often became darker brown than the rest of the leaf, appearing much like veins discolored through leaf infection by *Phytomonas malvacearum.* All such leaves were shed from the 70°-treated plant within a week; but they were retained somewhat longer (8–10 days) on the plants whose roots had been subjected to the 60° treatment. The youngest leaves showed no discolored areas and were retained longest. Some flowers opened quite normally, even after all but the very youngest leaves near the stem tip had fallen.

Roots that received the 70° treatment made no real growth subsequent to the treatment, although some of the tips enlarged noticeably, became bulbous, and retained their usual color for several days. All of them died and became brown within a week. Following the 60° treatment, some elongation of roots continued for several days; but the new root region formed was irregular in diameter and its apical portion tended to become bulbous, as when roots had been subjected to 10° for 4 hours. The older portions of the roots seemed to have been more severely affected by the treatment; they became dark brown and were apparently dead within a few days. After two weeks all roots were flaccid, gelatinous, and unquestionably dead.

Sections cut a week after the most severe treatment (70°) showed the xylem of the tap root to be dark brown, and brownish streaks were observed extending upward into the xylem of stem, branches, and petioles. Root cortex was obviously dead, but stem cortex was still green and showed no signs of injury. After a recovery period of three weeks, plants that had received the 60° treatment showed no discoloration of root xylem; but the root cortex was dead, excepting a small portion that had been above the level of the solution surface at the time of treatment. On the other hand, a brownish discoloration was evident in the xylem above the collet, in streaks which were progressively less pronounced farther up. In a 60°-treated plant sectioned after 12 days, some discoloration was present even in the petioles. All leaves on the 60° plants at the time of treatment dropped before the end of three weeks. At that time there were some weak green shoots arising from the lower portion of the main stem.

Injury induced by raising soil temperature to 60° C. or higher

Experiments in which the soil temperature was temporarily raised to 60° or 63° gave results similar to those obtained with the heat-treated solutions. On clear warm days, when the aerial surroundings were such as to produce relatively rapid transpiration, these heat treatments of plants in soil always produced pale or nearly white areas between the larger veins of the leaves while the treatment was in progress. More or less wilting usually occurred during the treatment; in several instances even the tips of the branches lost their turgidity. When the soil was cooled to greenhouse temperature immediately after the treatment, the discolored areas between the veins disappeared and the plants regained their turgidity. No sign of wilting or discoloration was present on the day after treatment, but after an additional day or two those leaves that had become severely discolored during treatment became flaccid and did not regain turgidity. All regions that had become discolored during treatment and had then apparently recovered became pale yellow again at this time, drying up and turning brown within several days. All such discolored leaves dropped from the plant within two weeks. Similar discolored areas appeared on leaves that had not wilted during treatment but had shown discoloration at that time. As in the solution cultures, these leaves soon became unusually rigid and leathery and later dropped from the plant.

A typical example may represent these experiments with heated soil. At 2:00 P.M., a healthy plant (soil temperature 40°, holard 60 per cent.) was transferred from the greenhouse bench to a 60° water bath. At 6:00 P.M. (soil temperature at the 4 cm. depth 56° in center and 65° near margin) the older leaves were severely wilted and there was a pronounced discoloration between veins in many unwilted leaves as well as in the wilted ones. The plant was then returned to the greenhouse bench, where it regained turgidity and the discolored areas disappeared within several hours. There were no visible abnormalities the day after the treatment. Most of the discolored areas, however, again became very conspicuous on the second day, reappearing as yellowish areas, which became dry and brown within a few days. Leaves, thus affected, fell within 10 days; but the young leaves on the plant at the time of treatment were still apparently healthy at the end of 3 weeks, during which period new leaves had formed at the tip of the main stem. On removing the plant from the soil at this time it was noted that all of the roots present at the time of treatment were dead, that the xylem throughout the root system was brown, and that this discoloration extended upward in the stem xylem for 12 cm. In spite of this severe injury, new roots were arising from the collet region immediately below the surface of the soil and new branches were forming on the main stem.

Discussion

References to the literature concerning the physiological effects of low soil temperatures may be found in the writings of KÖHNLEIN (**10**), WHITFIELD (**17**), PEIRCE (**16**), and CLEMENTS and MARTIN (**6**). It seems to be clear that wilting may be brought about, at least in a number of different plant forms, by a sufficient lowering of the root temperature in an adequately moist soil when transpiration is relatively rapid. CLEMENTS and MARTIN (**6**) induced visible wilting in sunflower at soil temperature of 4.5° (40° F.), but it required a still lower temperature to produce severe wilting. The only record of wilting at soil temperature above 4.5° appears to be that of KÖHNLEIN (**10**, p. 411), who noted partial wilting of sunflower at soil temperature of 17.5° or 18.5°, but the air temperature of his greenhouse was 42°; this is considerably higher than the air temperature prevailing when CLEMENTS and MARTIN noted wilting in the same plant and it is also considerably higher than the air temperature at which cotton plants wilted for the writer with soil temperature 20°. KÖHNLEIN also noted that his sunflower plants with soil at 18° wilted much more promptly than those with higher soil temperature in the same greenhouse.

It seemed remarkable that cotton plants wilted with root temperatures no lower than 18° under air conditions that were not unusually favorable for rapid transpiration, while they wilted at still higher root temperatures (20° to 21°) under air conditions that should have promoted unusually rapid transpiration. Different kinds of plants grown under similar conditions, and even plants of the same species grown under different environmental complexes, might be expected to wilt with different degrees of root cooling, even when all influential conditions except root temperature were quite healthful and alike at the time of wilting. It seems probable that, for any previously healthy individual plant, wilting induced by root cooling should occur with different degrees of cooling according to the combination of air temperature, air moisture, and radiation prevailing at the time of wilting. Such suppositions are based on the familiar consideration that wilting of this sort, which is immediately due to inadequacy of foliar moisture, is determined partly by the transpiration rate and partly by the rate at which water enters the leaves. In these root-cooling experiments the water-conducting capacity of the plants was surely not inadequate; neither was the environmental water supply inadequate, for the soil cultures were well supplied with soil moisture and the water supply in the solution cultures was practically infinite. It therefore seems safe to suppose that these cold-root wiltings were occasioned by inadequacy in the capacity of the root systems to receive sufficient water from without and to permit its rapid movement into the conducting channels.

The capacity of a root system to receive water from the soil solution is of course dependent partly on the extent of the absorbing surfaces, partly on the rate of water movement from root to stem (essentially the current transpiration rate in such plants as cotton), and partly on the more or less obscure conditions that are effective within the root tissue between the absorbing periphery and the conducting channels. Lowering the root temperature, as in these experiments, surely could not have reduced the extent of the root surface, nor did it increase the transpiration rate. Consequently it appears that the cold treatment either reduced the capacity of the root tissue to receive water from an adequate external supply or else reduced its capacity to let water move into the vessels.

As to the manner in which the living cortex of the absorbing region of the root might possibly be markedly more resistant to water passage at 10° to 20° than at 30° to 40° a number of different hypotheses might be suggested, but to test them logically would require quantitative experimental data that are not yet available. Two possible hypotheses may be mentioned in a roughly qualitative way: (1) A very simple hypothesis may be based on the temperature relation of the viscosity of water, which is about one and one-half times as great at 20° as at 40°. At a specified pressure gradient water moves through finely porous material more rapidly as the temperature is raised. The pressure gradient by which water moved through the root cortex into the xylem in the experiments of this study could not have been increased, since negative pressure in plants becomes more pronounced with the approach of wilting. It follows that a reason for the slower water movement at lower than at higher root temperatures, as shown in these experiments, is to be sought in increased resistance rather than in decreased pressure gradient. According to this hypothesis such increased resistance is considered as due wholly to change in water viscosity; the colloidal structure and arrangements of non-water materials in the root being assumed as not effectively altered when root temperature is lowered. For some experimental findings concerning the influence of water viscosity on water movement through porous porcelain reference may be made to CHRISTIANSEN, VEIHMEYER and GIVAN (**5**). The observations of BODE (**3**) on the effect of temperature on the passage of water from soil through the roots of the sunflower to the stem and those of KRAMER (**13**) on the absorption of water from the soil by porcelain cones lend support to this hypothesis. (2) The temperature relations of solation and gelation in colloidal material might be introduced as the basis for another qualitatively plausible hypothesis, if it is roughly supposed that the cortex cells interpose a greater resistance to water passage at lower than at higher temperature, not only because water is somewhat less fluid at lower temperatures but also because of changes in the ultramicroscopic arrangement, distribution, or configuration of their non-water material. Changes induced by lowering the temperature of the protoplasts may be readily supposed to render the entire tissue less permeable to water passage, as if the paths of water movement through them were narrowed or had become less numerous with decreasing temperature. Furthermore, it is at least logically possible that the ultramicroscopic porosity of the cell walls of the absorbing root cortex—including walls in immediate contact with the environmental water—may sometimes be reduced as the temperature is lowered.

It may be added that if the rate of water movement through the absorbing root cortex into the xylem (when the external water supply is adequate) is generally influenced by some sort of protoplasmic pumping action—as many writers have supposed—that action would be less effective as the water viscosity becomes greater and as permeability of the cortex and walls to water becomes less. Furthermore, the pumping action itself might be less vigorous at lower than at higher temperatures, which would be expected if such action really exists and if it is associated with respiratory activity—as suggested by LETA HENDERSON (**8**); for respiration is generally less rapid at lower than at higher temperature. But of course changes in cortex permeability—as those of solation and gelation—might be supposed to be greatly influenced by intensity of metabolic oxidation, whether pumping action is hypothesized or not. In this connection it is interesting to compare the soil temperature at which wilting occurred (20° to 21°) when conditions were favorable for rapid transpiration with the temperature relations of seed germination and subsequent growth in this tropical and subtropical species. CAMP and WALKER (**4**) and ARNDT (**1**) have observed that a soil temperature of about 27° was necessary for good top growth when air conditions were favorable, and FUNG (**7**) found that the optimal air temperature for top growth was 30° or higher. Some unpublished studies by the writer gave similar results. The writer has observed good root development at 24°, but then even at favorable air temperatures, top growth was retarded, as though the root systems were failing to supply the tops adequately with water or minerals, or both. Furthermore, germination percentage was found to be much reduced when the soil temperature was maintained at 18° to 19° (**4**, table IV; **1**), which is about the same as the minimal soil temperature at which the cotyledons could be raised above the soil surface. With a soil temperature between 18° and 20° the cotyledons that did appear above the soil remained yellow for a week or longer, as though the roots were not supplying requisite materials at an adequate rate. It is thus seen that the critical soil temperature for wilting of cotton in the cold treatments described in this paper is not greatly different from what has been found to be the minimal temperature for healthy seed germination and seedling development, while it is only slightly below the soil temperature necessary for healthy root growth.

The results here presented on the effects of lethal high temperatures when applied to previously healthy plants are in essential agreement with previous observations, as reported for cotton and other plants by KRAMER (**12**), but the present account adds observations on previously unreported wilting of leaves at the time of the treatment, also on the bleaching of regions between the veins while heat treatment was in progress, and on the subsequent history of these injured regions. Wilting was observed while the heat treatment was being applied (a) when the solution was heated to 70° and maintained at that temperature for 15 minutes, also (b) when the soil temperature was raised to 56° or 65° (four hours being required to reach 56° in the center of the soil container after it had been placed in a 65° water bath). That this wilting was not due to heat effect on water viscosity is obvious. It is also obvious that whatever caused this loss of leaf turgor ceased to be operative shortly after the root temperature was reduced to 36°, for the treated plants soon recovered. It appears, however, that the rate of movement of water through the cortex was, in those cases, temporarily lowered in some way during heat treatment. This may suggest a reversible change of some kind in the root tissues, but since there is little information available in this connection it would be premature to attempt hypotheses concerning the possible nature of such a change.

That killing most of the root system by heat did not immediately reduce transpiration considerably (and subsequently reduced it only slowly) renders it probable that dead or severely heat-injured roots were still sufficiently absorptive and sufficiently permeable to water to keep the foliage adequately supplied for a considerable period. If some kind of pumping action dependent on healthy protoplasm in the roots were necessary for maintaining the transpiration stream at an adequate rate it might be expected that wilting should occur promptly with the application of heat to the root system, without the maintenance of the original transpiration rate for a day or more thereafter. For a somewhat thorough discussion of a similar problem to the one here suggested, reference may be made to OVERTON (**14, 15**) and KRAMER (**11, 12**). It is clearly apparent that the vessels of the heat-treated plants did not become seriously plugged—as by gum deposits—during the heat treatments nor for at least a day or two thereafter. They may have become plugged still later. BERKLEY and BERKLEY (**2**) observed that water still passed upward rapidly through the stems and petioles of their cotton plants after these organs had been killed by high air temperatures. Some time after the roots were killed their previously living cells must have collapsed completely, but their coarser structure was apparently maintained as long as the original transpiration rate was not greatly reduced. Otherwise, it is difficult to imagine them maintaining adequate capillary contact with the moisture films of the soil.

Discoloration of the areas of the older leaves while the roots were receiving the injurious or lethal heat treatment may not have been due to an inadequate water supply of the leaves. When cotton plants wilted from the effects of drought, discoloration did not regularly occur and did not appear in plants wilted by application of low temperatures to the roots; but the discoloration here described was not unlike the permanent bleaching that may be produced by exposing cotton leaves to lethal air temperature, nor is it unlike the discoloration (called "scald" by the cotton farmer) that appears at times on leaves of cotton plants infected with *Fusarium vasinfectum.* The leaf discoloration that accompanied heat treatment of the roots was superficially suggestive of poisoning. Some sort of mildly toxic material formed in the heat-injured cells of the roots may perhaps have been promptly carried to the lower leaves in the transpiration stream—or possibly in the phloem. If such a supposition is tenable it must be supposed further that the first mildly injurious effect in restricted regions of the older leaves was not lethal and was reversible, for the discolored areas between the veins vanished within a few hours after the heat treatment was discontinued—within 90 min. in one experiment, in which the leaves had not wilted. Perhaps if the heat treatments had been more severe or longer continued such spots would not have regained their normal green color. At all events it seems quite possible that this early discoloration was due to some toxic material that arose in or near the heated roots and was carried upward quickly, that its delivery in the leaves ceased or became much slower very soon after heating was discontinued, and that its localized injurious effects in the foliar tissue were reversible in rather prompt recovery.

The second appearance of localized foliar discoloration, in the same areas as those previously discolored, also resembled some discolorations produced by poisons—for example, that produced by toxic concentrations of SO_2 on alfalfa in the experiments of HILL and THOMAS (9). This second discoloration sometimes first appeared as small, light brown spots (1 to 2 mm. in diameter), which rapidly coalesced to involve the entire area between adjacent large veins; the discoloration finally spread to the veins, as already noted. A similar discoloration of the leaves was noted on the cold-treated plants, but only when the temperature was lowered to 10°, which temperature was also sufficiently injurious to cause abnormal root development. In these latter plants, as contrasted to the heat-treated ones, the young leaves near the top of the plant, which had not yet attained full development, were the first to show discoloration.

By the time of the second appearance of the brown areas on the leaves of plants whose roots had been heated, cell disintegration in the killed roots may have become greatly advanced and toxic material arising therein may have been of a more virulent type or more plentiful, or both, than during the short period of the heat treatment. The upward movement of such material might continue indefinitely, soon leading to local necroses in the affected leaves and to their eventual death. If these suppositions were approximately correct, it might be said, following OVERTON (**15**), of the affected regions and finally of these entire leaves, that they dried out because of death rather than that they died because of an inadequate water supply. It is, of course, not necessary to suppose the toxic material of the first evanescent discoloration during the period of heat treatment to have been at all of the same sort as that involved in the subsequent effects. It might be expected that the later injury should appear most promptly in tissues of localized regions that had been previously slightly affected and had apparently recovered; perhaps those tissues were originally unusually susceptible to injury of this sort and their recovery from the first poisoning may have been incomplete.

The brown stain, which soon appeared in the xylem of roots, stems, and even petioles of the heat-treated plants and its greater intensity and upward extent as the heat treatment was made more severe, may be taken as evidence that unusual material of some sort had passed upward from roots to foliage, for such stain has not been found in healthy plants. Discoloration immediately above the collet (*i.e.*, just above the most severely treated region) was usually darker than in the roots. It may be supposed that soluble substances not usually present in the transpiration stream were carried upward from the injured root systems, that some of these produced stain in the xylem vessels—perhaps also toxic effects in living cells of that tissue—and that some of them were responsible, first for localized injury in the leaves and then for the death of foliar tissue.

In connection with these hypothetical considerations concerning possible effects of toxic emanations from roots that had been killed or severely injured by heat treatment, some special attention should be given to the clearly differentiated but somewhat similar symptoms of leaf injury that followed excessive cooling of roots in these studies. Those symptoms were confined to the younger leaves, near the top of the plant, while it was the older leaves that were injured by excessive heating of roots. When the cold treatments were severe enough to cause abnormal root development (approximately 10°), the younger leaves were apt to show narrow regions of killed tissue at their margins on the day following the treatment and several days later yellowish areas between the veins. There was no recovery of the marginal tissues, but the yellow areas between veins shortly disappeared, not leading to defoliation. The marginal injuries suggest effects of water deficiency and they might be regarded as analogous to tip burn. But the evanescent discoloration following cold treatment of the roots can hardly be attributed solely to excessive water deficit in localized regions, for such discoloration of young leaves is not commonly observed when plants are injured by ordinary drought when in the field. Perhaps these discolorations may indicate some form of mild poisoning, and it is at least logically possible to relate them tentatively to local accumulations—enhanced by foliar water deficit and transpiration—of toxic materials emanating from the injured roots. It will be recalled that these cold-treated plants exhibited some injury at the root tips and that the subsequent growth of many tips indicated physiological disturbance such as might result from disturbed metabolism and resultant toxic action.

Summary

1. Cotton plants growing in the greenhouse wilted on clear days when the temperature of the roots was sufficiently lowered for a short time. Solution cultures showed this wilting when their temperature had been lowered to between 10° and 18° C.; for soil cultures, with ample water supply, the highest soil temperature at which wilting occurred was generally somewhat higher, between 17° and 20°. The amount of this lowering necessary to produce wilting varied, being clearly dependent on air temperature, relative humidity, and sunlight intensity.

2. Exposure of the roots of plants growing in solution or soil cultures to a temperature of 60° for 60 min. severely injured the roots and caused a marked reduction in the absorption of water by such plants. Plants in solution cultures did not wilt while being heated to 60° in 60 min. A temperature of 70° maintained for 15 min., however, did cause similar plants to wilt. Plants growing in soil wilted at a soil temperature of 60°. White areas appeared between the veins of the leaves during the heat treatments at 60° and higher. These discolored areas disappeared within several hours after the reduction of the soil temperature, only to reappear several days later as yellow or brown regions in which the tissues became dry and died. Leaves thus affected dropped from the plants within 12 days.

3. The distal portions of some of the roots of plants in solution cultures were still capable of some limited elongation after an exposure to 60° for 60 min. The newly formed parts were, however, irregular in diameter and the roots became flaccid and gelatinous after several days. Exposure of roots to 10° for several hours caused them to lose their geotropic sensitivity, resulted in partial inhibition of growth in the apical portions, and produced

an abnormal bending and distortion of such new growth as did arise from the injured apices.

4. It is apparent that cooling of the roots produced wilting through lowering the capacity of those organs to absorb water from without and to transmit it to the conducting channels. Such lowering might be occasioned, to some extent at least, through increase in the viscosity of water, which accompanies cooling; also it might result from a decrease in permeability of root protoplasts or cell walls, due to lowered temperature; or it might result from retardation of some physiological activity of the root cortex (pumping action) induced by cooling. Wilting that occurred while the roots were at an injuriously high temperature may have been occasioned through lowered permeability of the root cortex or through production and upward movement of some sort of toxic material. Slight permanent leaf injury due to cold treatment of roots may perhaps have been due to inadequate water supply while the treatment was in progress, or possibly to toxic material. But the pronounced leaf injury and death of leaf tissues that followed several days after the heat treatment appears to have been due to injurious substances produced in the roots (most of which had been killed by the treatment) or possibly in the adjacent soil. This supposition is supported by the observation that death of heat-treated roots and post-mortem changes therein were accompanied and followed by pronounced discoloration of the stem xylem, which had not been heated.

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