RANGE OF SOIL-MOISTURE PERCENTAGES THROUGH WHICH PLANTS UNDERGO PERMANENT WILTING IN SOME SOILS FROM SEMIARID IRRIGATED AREAS

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INTRODUCTION

It has long been known that the wilting coefficient, or wilting point, of a soil does not represent the lower limit of soil moisture available to plants but rather the approximate lower limit available for growth (6). Some writers, however, have used the term rather loosely to refer to the percentage of nonavailable moisture, possibly on the assumption that the amount of moisture available at moisture percentages below the wilting point is so small as to be of no practical significance.

Alway (1), Batchelor and Reed (5), and others have reported finding soil under deep-rooted trees or shrubs at moisture percentages well below the wilting coefficient and in some cases at about the hygroscopic coefficient. These writers pointed out the significance of the moisture below the wilting coefficient in the maintenance of life in these plants during periods of prolonged drought, and Batchelor and Reed proposed that, since the wilting coefficient does not represent the lower limit of available moisture, the hygroscopic coefficient be used as the reference value for expressing the relative wetness of a soil as related to plant behavior. While the hygroscopic coefficient, in the sense in which this term was employed, is no longer in general use as a soil-moisture constant, Batchelor and Reed's contention that a soil-moisture constant, approximately equivalent to the nonavailable soil-moisture percentage, is needed, is nevertheless a pertinent one.

In recent investigations of the response of citrus trees to various soil-moisture conditions (10), it was found that the water deficit of trees in the field was related not only to the proportion of soil in the root zone that was reduced to the first permanent wilting point, but also to the extent to which the moisture content of the drier parts of the soil in the root zone was reduced into the wilting range.

The wilting range is the range in soil-moisture percentages in which plants undergo progressive permanent, or irreversible, wilting, from
wilting of the oldest leaves to complete wilting of all the leaves. The lower end of this range has been termed the "ultimate wilting point." In this paper wilting is called permanent if turgor is not regained by the uninjured leaves when the plant is kept in an approximately saturated atmosphere in a dark humid chamber for 14 to 16 hours.

The terms "wilting range" and "ultimate wilting point" were introduced by Taylor, et al. (17) to describe the soil-moisture conditions in plots of native California shrubs, where they found that the soil-moisture content, to a depth of 6 feet or more, was appreciably below the first permanent wilting point at the end of the dry season. They defined the wilting range as the range in moisture content of the soil between the wilting coefficient and the ultimate wilting point, and the ultimate wilting point as the moisture content at which all the leaves remain completely wilted in a humid atmosphere. That is, the ultimate wilting point represents approximately the lower limit of the range of soil-moisture percentages in which plants are able to maintain life, though at this stage many of the leaves and probably some of the roots are dead. Even at the ultimate wilting point a small amount of soil moisture is, of course, still available to living tissue, and it might be supposed that the logical end point in determining the available moisture held by a soil would be the soil-moisture percentage at which the process of dying had just been completed.

Such determinations would, however, be time consuming, and the time when death was complete would be uncertain; furthermore the percentage of moisture at the death point is numerically practically the same as that at the ultimate wilting point, though, of course, at such low moisture percentages a small change in moisture represents a relatively large change in the vapor pressure or moisture tension of the soil.

Since the first permanent wilting point, or wilting coefficient, corresponds to approximately the soil-moisture percentage at which elongation ceases, and since the ultimate wilting point represents practically the lower limit of soil moisture that can be utilized by the plant in maintaining life, it would seem that in studies dealing primarily with the response of plants to soil-moisture deficiency these two reference values should provide adequate bases for comparison with most soil-moisture conditions encountered.

The wilting range, as here defined, has been reported for only a few soils (10, 17). Since more general information was needed in connection with irrigation experiments, it seemed desirable to determine the wilting range of a large number of soil types varying widely in texture and other characteristics.

METHODS

Samples of about 80 soils, representing about 50 soil types as shown on soil survey maps of several areas of southern California, were collected for the study. With few exceptions the soil samples were taken from the top foot of soil, and most of them were from cultivated, irrigated orchards or fields. A few samples were from uncultivated desert lands or brushlands. The samples were air-dried and screened through a 2-mm. round-hole screen.
Moisture-equivalent determinations were carried out with standard apparatus, and the precautions recommended by Veihmeyer et al. (19) were observed. Four samples of each soil were run, and the average was taken as the moisture equivalent. In a few instances in which the four samples showed unsatisfactory agreement the determinations were repeated.

The wilting range determinations were made during the period from September 1940 to May 1941 at Pomona, Calif. The procedure for determining the wilting range is simple, but certain precautions were found to be necessary in order to obtain reliable results. The method employed proved to be convenient, economical of time, and reasonably reliable. Ten cultures with each soil sample, 5 for the determination of first permanent wilting and 5 for the determination of ultimate wilting, were run. The plant containers used were pint, compression-top cans, with %4-inch holes punched in the centers of the covers. Four or five hundred grams of soil, depending upon the volume weight, was weighed into each can. Weighings were made on a spring food balance of 1-kg. capacity, and the groups of 10 cultures were placed on flat trays on the greenhouse bench. Russian Giant sunflower (Helianthus annuus L.) seedlings which had just shed the seed coats were transferred from flats of sand to the soil culture, 1 plant to a can.

It was found that frequently plant growth was poor unless care was taken to maintain ample soil pore space in the cultures. Jarring the cans after filling them caused appreciable settling of both dry and wet soil; so when the seedlings were transplanted to the cans, all the soil was poured out of the culture can into another container and then poured back into the can through a funnel while the plant was centered in the can by means of a small planting guide shown in figure 1, A. The roots of the seedlings were dipped into a soil suspension just before they were planted. This coating of the roots with a thin layer of fine soil at planting hastened recovery from transplanting. This improvement in recovery must have resulted either from protecting the absorbing surfaces from momentary drying or from improving contact between soil and roots, since it was found that regardless of treatment, the old root tips did not resume growth after transplanting but that new root growth arose from lateral root initials, which appeared about 2 days after transplanting.

After the seedlings were planted, the surface of the soil in the can was covered by a layer of absorbent cotton and the lid was fitted in place; then the culture was placed on the spring balance, and the weight of water required to wet the cotton, plus the calculated amount required to raise the moisture content of the soil to field capacity, was added from an overhead supply bottle. The cotton was placed on the soil surface to protect it from being puddled when water was added and to encourage the development of roots in the surface layer of soil. To loams and clays, nitrogen (50 to 100 parts per million of soil) was added in the water at planting and a small amount of monopotassium phosphate (KH₂PO₄) was mixed with the dry soil before planting. The sands were watered at planting with a complete nutrient solution. The first set of cultures run were fertilized with nitrogen only, and determinations on some of these soils had to be repeated because the lower leaves were severely affected by symptoms of malnutrition and failed to show normal recovery after temporary
Figure 1.—A, Transplanting seedling to culture can; B, plant that had recovered turgor in the humid chamber after being wilted; C, plant at first permanent wilting point; D, plant at ultimate wilting point.
wilting. For a day after planting, the cultures were protected by a cloth shade, and then they were grown in full sun until the third pair of leaves had reached almost full size. Whenever some of the plants of a group in the same soil showed temporary wilting, water was added in sufficient quantity to bring the soil up to the estimated weight at field capacity, allowance being made for the increasing weight of the plants in estimating the quantity of water needed. When the third pair of leaves was almost fully developed, the soil was wetted to the estimated field capacity, the lid opening around the stem was closed with cotton, and watering was discontinued. As soon as cultures showed temporary wilting of the first pairs of leaves, they were placed under a cloth shelter, where they usually recovered turgor unless the leaves had been injured by fungus infection or malnutrition.

The lowest pair of leaves of a plant inadvertently left in full sun until several pairs were badly wilted usually showed injury and failed to recover turgor. Such plants could not be used for determining the first permanent wilting point.

When the lowest one or two pairs of leaves of cultures used for determining the first permanent wilting point wilted under the cloth shelter, the cultures were transferred to a dark humid chamber. High humidity was insured by exposing a large water surface in the chamber; in addition, just before the chamber was closed, the air was filled with a fine mist from a hand sprayer. As the plants recovered turgor, they were returned to the cloth shelter. This procedure of transferring the cultures back and forth from cloth shelter to humid chamber was continued until the basal pair of true leaves failed to recover after being in the humid chamber overnight. At this stage the tips of the second pair of leaves usually showed partial loss of turgor and drooped slightly. During the course of this process the time required under the cloth shelter before temporary wilting was induced gradually shortened until finally only a few minutes were required, and conversely the time required for recovery increased until finally recovery failed to occur within the overnight period of 14 to 16 hours. Since large numbers of plants can be transferred at one time, the labor involved in handling cultures in this manner is not prohibitive. The appearance of typical plants after recovery from temporary wilting and at the first permanent wilting point is shown in figure 1, B and C.

After the cultures used for determinations of the first permanent wilting point were watered for the last time, measurements of the stems were made early each morning with a ruler fitted with a sliding sidearm which could be brought into firm contact with the terminal growing point. Stem length was measured with an error of only about 1 mm. It was found that cessation of stem elongation coincides approximately with first permanent wilting as judged by the condition of the basal pair of leaves of normal plants. There was, however, some variability; some vigorously vegetative plants continued to elongate several millimeters a day for 1 or 2 days after the lower leaves were judged to be flaccid at the end of the 14- to 16-hour period in the humid chamber. Since, however, this rate of growth was very low as compared with the normal rate when the cultures were first sealed, approximate cessation of stem elongation was used as a secondary
criterion of first permanent wilting and was especially useful with plants that had suffered some injury of the lower leaves but were not so badly injured as to be considered unsuitable for use.

The cultures used for determining the ultimate wilting point were left under the cloth shelter until the apical leaves were badly wilted. Unless the apical leaves are severely wilted, it is difficult to tell whether they show recovery in the humid chamber. At this stage the stems were frequently flattened and distorted and the older leaves were dead. When placed in the humid chamber they never showed more than very slight signs of recovery of even the apical leaves. The appearance of a typical plant at the ultimate wilting point is shown in figure 1, D. At the ultimate wilting point the terminal one or two pairs of leaves, the terminal growing point, and at least some of the axillary buds are alive and the plant will resume growth if the soil is wetted.

When the plants were judged to be at the first permanent wilting point or at the ultimate wilting point, they were pulled out of the soil so that the largest roots were removed. The top layer (about one-half inch) of soil, in which root concentration was usually low, was removed and discarded. The soil from the upper and lower halves of the culture cans was sampled separately. The moisture content, determined as loss under drying at 105° C., is expressed as percentage of dry weight. A comparison of the values for the two samples served as a convenient check on possible errors in manipulations or calculations, but the average of the two was taken as the moisture content of the culture, and the average of the five cultures was taken as the moisture percentage at the first permanent or at the ultimate wilting point. The moisture content of the soil from the lower halves of the cultures was usually 0.1 to 0.3 percent higher than that from the upper halves. This difference may have resulted from differences in root concentration, soil temperature, salt concentration, or loss by evaporation, but the cause was not determined.

The widest variations between the moisture percentages of the five cultures of a sample at the first permanent wilting point or at the ultimate wilting point ranged from about 0.3 in sands to as much as 2.1 in the heaviest clay. These variations resulted in part from variations in judgment of the several workers who handled the cultures and in part from unavoidable variations in severity of wilting before the plants were placed in the humid chamber for the last time. Slight variation may be expected also as a result of variability in the amount of mechanical tissue in plants grown under different conditions of nutrition, water supply, temperature, and other environmental factors.

In the literature wilting-point values are sometimes reported to hundredths of a percent of moisture, and usually the probable or standard errors reported are small. Perhaps such data imply that the methods used in wilting-point determinations lend themselves to greater precision and reproducibility than may actually be the case. It is to be expected that variations between individual cultures of one soil run at the same time by one worker will be small, but over a period of several months or years an individual worker's notion of what the plant looks like at some selected stage of wilting, as first permanent wilting or ultimate wilting, may vary considerably unless some well-
defined criteria are established for judging when the selected stage has been reached, and it is almost certain that the stage of wilting classed as permanent wilt has varied widely as judged by different workers in widely separated laboratories.

To obtain an indication of the variability which might be expected in wilting points run on the same sample of soil at different times, cultures from a large sample of clay loam were run through the usual procedure in the fall, winter, and spring along with other soils, so that only the usual care would be given them. The average values obtained for first permanent wilting point in fall, winter, and spring were, respectively, 19.9, 20.2, 20.3; and for ultimate wilting point, 17.3, 16.9, 17.0. The difference between the extremes in each case was 0.4 percent. That rather consistent results may be obtained in routine wilting-point determinations by the procedure described was demonstrated by the results obtained on samples from 12 field plots on a relatively uniform clay loam. Each sample was an unscreened composite of eight 4-inch auger borings distributed uniformly over each of the plots, which were about 160 feet long and 24 feet wide. The first permanent wilting points of the 12 samples ranged from 20.3 to 21.9, and the moisture equivalent ranged from 32.7 to 36.1. In routine field work the average value of first wilting point or ultimate wilting point for these plots might be used for any one of the plots without serious error.

The precautions found to be helpful in obtaining reliable first permanent wilting points may be summarized as follows:

1. Good root growth and distribution should be obtained by maintaining ample pore spaces in the soil and avoiding wetting the soil far above field capacity.

2. Vigorous and healthy plants should be obtained by maintaining favorable nutrition, preventing infection by fungi, and avoiding overheating of the soil in culture cans exposed to full sunlight.

3. When the plants wilt, they should be placed in the humid chamber before excessive desiccation causes injury to the lower leaves.

4. Daily measurements of stem elongation should be made as a supplementary indication of first permanent wilting. Basal leaves that have become senescent or have been injured, even though not showing obvious signs of injury, may fail to recover when the plant is still receiving enough water to cause appreciable growth. Plants elongating at a rate of more than about 10 or 15 percent of the rate maintained during the first 1 or 2 days after the final watering should probably not be considered as permanently wilted.

RESULTS

PLANT RESPONSE TO DECREASING SOIL MOISTURE

In general, the daily rate of stem elongation decreased soon after the cultures were sealed and watering was discontinued, but no definite conclusions as to the relation between growth rate and soil moisture above the wilting range can be made, because as soon as temporary wilting occurred the plants were placed in partial shade and part of the time in a dark humid chamber. It is clear, however, that even under these conditions elongation had almost or entirely ceased at the first permanent wilting point. Growth rate curves typical of the plants grown in soils of different textures ranging from sand to clay
are shown in figure 2. Measurements of stem elongation were also made on a number of plants used in determining the ultimate wilting point. These plants were placed under the cloth shelter when they first became temporarily wilted, but were not placed in the humid chamber until all the leaves were severely wilted. Elongation had approximately ceased when the basal leaves remained wilted overnight, and the stems, because of water loss, decreased in length before the ultimate wilting point was reached.

![Graph showing daily rate of stem elongation of sunflower plants in different soils accompanying decrease in soil moisture from field capacity (when growth measurements were begun) to first permanent wilting point (when last measurements were taken). Moisture equivalents (M.E.) given.](image)
An attempt to estimate the changes in force exerted on water at the root surface during the progress of the decrease in moisture content of the soil from about the field capacity to the ultimate wilting point was made by determining the freezing point of samples of sap pressed from the plant tops and then calculating the equivalent osmotic pressure corresponding to the freezing-point depression. The plant tissue was kept frozen until just before the sap was extracted in a hydraulic press. Samples were taken from plants under two sets of conditions. One set of cultures was wetted to above field capacity and sampled at intervals as the soil dried out. The forces acting on the water in plant and soil were not brought to equilibrium by placing the cultures in a humid chamber; but the force gradient between plant and soil was comparable with that in the field at sunrise, since the

plants were placed in a room overnight where the relative humidity was only slightly less than that of the outside air and then were sampled after a night of relatively low transpiration. The calculated osmotic pressure of samples of sap from these cultures is shown by the upper curve in figure 3.

These data (fig. 3, upper curve) show that as the moisture content of the soil decreased from about 24 percent to the lowest value reached, about 17 percent, there was a definite increase in the osmotic pressure of sap. Moisture determinations made on plant tops from these cultures showed that with decreasing soil moisture there was a concurrent decrease in moisture content of tissue. It is apparent that there

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**Figure 3.** Osmotic pressure of expressed sap from sunflower plants in soil at different soil-moisture percentages. Upper curve: Plants continuously in dry air; sampled at end of the dark period. Lower curve: Plants sampled after 16 to 24 hours in humid chamber.
is a progressive change in the slope of the curve as the moisture content of the soil decreases below about 24 percent, but there is not a sharply defined break at 18.4 percent, the first permanent wilting point. At soil-moisture percentages several percent above the first permanent wilting point, the basal leaves of these plants failed to recover turgor during the night. It is clear that these plants, grown under atmospheric conditions resembling those in the field but with the roots rather uniformly distributed throughout a small mass of soil, were subjected to progressively increasing water deficit from a soil-moisture percentage about halfway between the moisture equivalent and the first permanent wilting point to a value below the latter.

The second set of cultures was sampled at only 3 different soil-moisture percentages. This set of cultures was divided into 3 groups. One group of 3 cultures was sampled at a soil-moisture percentage slightly above field capacity; another, of 17 cultures, at the first permanent wilting point; and a third, of 18 cultures, at the ultimate wilting point. The force gradient from plant to soil was presumably reduced to a very low value by placing these cultures in approximately saturated air for a period of 16 to 24 hours just before sampling. The cultures used for first permanent wilt were in the humid chamber most of the time for several days prior to sampling as well as for the last 16 to 24 hours. The cultures sampled at field capacity were presumably at full turgor.

The calculated osmotic pressures of the sap from plants at full turgor ranged from 6.4 to 6.8 atmospheres and averaged 6.6 atmospheres; at the first permanent wilting point the osmotic pressures ranged from 8.4 to 10.3 and averaged 9.1 atmospheres; and at the ultimate wilting point they ranged from 18.8 to 24.3 and averaged 22.2 atmospheres. The average values at full turgor, at the first permanent wilting point, and at the ultimate wilting point are shown as an assumed curve (lower curve) in figure 3.

The value of freezing-point determinations on expressed sap as an indirect measure of the forces acting on water at the root surface may be questioned, since the sap was extracted from the plant tops rather than from the roots and the wall pressure of the cells was not known. In spite of these apparent shortcomings, however, it seems probable that the method is fairly reliable. Water is translocated from one part of the plant to another so readily that apparently little difference in diffusion-pressure deficit exists in different parts of the plant unless transpiration is quite active (2, 9). Therefore, there was probably very little difference between the diffusion-pressure deficits of tops and roots of the plants that were kept in the humid chamber most of the time for several days before sampling.

Under most conditions determinations of the osmotic pressure of expressed sap give no indication of the diffusion-pressure deficit of the tissues from which the sap was taken. In this instance, however, it may reasonably be assumed that at full turgor the wall pressure just equaled the osmotic pressure and that therefore the diffusion-pressure deficit was approximately zero. At the first permanent wilting point the wall pressure of the cells in the basal leaves was approximately zero, and the diffusion-pressure deficit was therefore approximately equal to the osmotic pressure. The diffusion-pressure deficit of the remainder of the plant top must have been equal to that of the lower
leaves and the osmotic pressure slightly higher than that of the basal leaves, since the upper leaves were at least partially turgid. It seems reasonable to assume that the diffusion-pressure deficit of the roots at the first permanent wilting point was somewhat, but not greatly, less than the osmotic pressure observed in the samples of sap expressed from the tops. At the ultimate wilting point wall pressure was probably zero, and the diffusion-pressure deficit was equivalent to the osmotic pressure. The marked increase in the osmotic pressure of sap, as the soil dried out from field capacity to the ultimate wilting point, undoubtedly resulted principally from loss of water by the tissue rather than from an increase in solutes. The average moisture content of plant tops, expressed as grams of water per gram of dry matter, was in plants at full turgor, 10.49; at the first permanent wilting point, 8.88; and at the ultimate wilting point, 5.24. The freezing-point determinations, then, indicate that the force with which water in soil at the root surface was held at the first permanent wilting point amounts to somewhat less than 9.1 atmospheres, and at the ultimate wilting point to about 22.2 atmospheres. These values, expressed in terms of soil-moisture tension, would indicate that, in soils practically free of salts, the tension at the first permanent wilting point may be somewhat less than 9,400 cm. of water (pF 3.97), and at the ultimate wilting point the tension may be about 22,900 cm. of water (pF 4.36).

From a comparison of the general level and change of slope of the curves in figure 3, it appears that at soil-moisture percentages between the moisture equivalent and the first permanent wilting point, the osmotic pressure of sap of the plants held in nonhumidified air was affected by transpiration. The state of turgor of leaves and the osmotic pressure of sap of these plants at soil moisture 2 or 3 percent above the first permanent wilting point were about the same as that of the plants from the humid air with soil moisture at the first permanent wilting point. When the soil moisture of both series of plants was at the first permanent wilting point, the difference in turgor and in osmotic pressure of sap of the two groups was quite large. With the decrease in soil moisture from field capacity to the first permanent wilting point, the increase in the osmotic pressure of the sap was about 5 atmospheres in the plants held in nonhumidified air but only 2.5 atmospheres in plants held in humid air. Apparently, when plants are held under conditions that permit water loss, even though the rate of loss is relatively low, as it was in this instance, there is some lag of absorption behind transpiration. At soil-moisture percentages near or in the wilting range the departure from equilibrium between the forces acting on the water in plant and soil may be large. Apparently, to obtain reliable values for the first permanent wilting point, it is essential that the cultures be handled in such a manner that the lower leaves just remain flaccid and that the second pair recover at least partial turgor when the forces acting on water in plant and soil are at approximate equilibrium.

When such conditions of equilibrium exist, the force with which water is held by soil at the root surface is, at the first permanent wilting point, probably nearly equal to the diffusion-pressure deficit of the basal leaves, and at this stage the turgor of cells in the growing regions has been reduced to the point at which further elongation does not take place or proceeds very slowly. First permanent, or irre-
versible, wilting is then a fairly well-defined stage in the progressive changes that occur in young healthy sunflower plants grown under certain specified conditions, and this stage is reached by all such plants in the same soil at approximately the same soil-moisture percentage. It should be clear, however, that the well-defined end point at the first permanent wilting point of the soil is well defined only so far as the response of the plant is concerned and only if the plant-soil system is at approximate equilibrium. The first permanent wilting point does not mark a point of abrupt change in the state or properties of the water in the soil. It has been supposed by some writers that there is a sharp break in the continuity of the water columns or films in the soil at the first permanent wilting point. Maximov (11, p. 79) suggested that “... even with the slowest rate of water absorption, the moment at last arrives when the water films in the drying soil are ruptured, and the water loses its mobility; this moment corresponds to the wilting coefficient.” The fact that an appreciable amount of water is extracted by the plant at soil-moisture percentages between the first permanent wilting point and the ultimate wilting point indicates that there is not an abrupt cessation of water movement at the first permanent wilting point.

It is highly probable that root extension as well as stem elongation is negligible at soil-moisture percentages below the first permanent wilting point and that the extraction of moisture in the wilting range is dependent almost entirely on water movement to the roots. Diffusion of water vapor probably accounts for a part of this movement, but the results recently obtained by Richards (13) and Richards and Weaver (14) indicate that moisture transfer at rates higher than can be accounted for by gaseous diffusion occurs in soils at moisture percentages in the wilting range when pressures at the membrane surface are comparable in magnitude to the estimated diffusion-pressure deficits of roots in soil in the wilting range. Richards found that at a pressure of 16 atmospheres the moisture content of 5- to 10-mm. layers of soil was reduced from saturation to moisture percentages in the wilting range in 24 to 36 hours.

It has also been supposed that at the first permanent wilting point the force with which water is held by the drying soil increases so sharply that significant amounts of water cannot be extracted by the plant beyond this point, and that consequently the stage or degree of permanent wilting selected as the end point in wilting-point determinations is of slight importance. Vapor-pressure curves of soils are usually shown for a wide range of soil-moisture percentages, such as that from the moisture equivalent to the air-dry or oven-dry state, and over such a range the change in the slope of the curve appears sharp indeed in the region of the first permanent wilting point. It may be noted, however, from figure 3 that the break in the osmotic-pressure curve also is relatively sharp in the same region and that the increase of about 13 atmospheres in osmotic pressure, and presumably in diffusion-pressure deficit, between the first permanent wilting point and the ultimate wilting point results in the absorption of appreciable amounts of water at soil-moisture percentages below the first permanent wilting point, although it is true that below that point the rate of absorption is low.
WILTING RANGE AND ITS RELATION TO AVAILABLE RANGE, MOISTURE EQUIVALENT, AND PERCENTAGE OF SOIL COLLOIDS

The first permanent and the ultimate wilting points of the soils used in this study are shown plotted against the moisture equivalent in figure 4.

In general, the magnitude of the wilting range increases with increasing fineness of texture, as indicated by the moisture equivalent, but this relation is by no means consistent. Some soils of nearly the same moisture equivalent vary appreciably in magnitude of the wilting range.

The differences in magnitude of the wilting range are apparently largely determined by the moisture-retaining characteristics of the different soils at soil-moisture tensions in the wilting range, though other factors, such as osmotic pressure of the soil solution, are probably involved. The moisture-retention characteristics have been determined on duplicate samples of many of these soils by Richards and Weaver (14). The slope of their moisture-retention curves at tensions in the region of the wilting range shows that, in general, for a unit change in tension the magnitude of the change in moisture percentage of the soil increases with increasing fineness of texture, but this relation, like that between wilting range and texture, is not consistent. That is, the moisture-retention curves of some soils of about the same moisture equivalent cross in the region of the wilting range.
The soil moisture within the wilting range provides the plant with an emergency reservoir that enables many species of plants to survive periods of prolonged drought or to mature seed after vegetative growth has ceased as a result of water shortage. With the reduction in the rate of absorption, which occurs near the first permanent wilting point, and the severe water shortage that follows, the various mechanisms by which transpiration is greatly reduced, such as stomatal closure and abscission of leaves, are set in motion; but after these changes are in progress there still remains the available water of the wilting range, which may be slowly absorbed over a relatively long period. Since the magnitude of the wilting range of different soils, even though they may be of similar texture, varies widely, it seems likely that this characteristic of a soil may be of some importance among those factors that effect the survival of plants during periods of drought. It is true, however, that the differences in magnitude of the wilting range of coarse- and fine-textured soils would be less, because of the greater volume weight of the coarse-textured soils, if the wilting range were expressed as moisture per unit volume of soil rather than as percentage of dry weight.

Perhaps the importance of the wilting range in the water economy of the plant may be evaluated most readily by a comparison of the wilting range and the range of soil moisture available to the plant. The approximate percentage of the available moisture that is held in the wilting range of soils of various moisture equivalents is shown in figure 5. The approximate available range is assumed to be the moisture held between the ultimate wilting point and the moisture equivalent. This assumption is not strictly correct, since the moisture equivalent is slightly higher in clays and appreciably lower in sands than the field capacity; but the moisture equivalent has been widely used as an approximation of field capacity, and, since it may be considered as a soil-moisture constant, determined by a standardized method, whereas the field capacity is not a constant but is affected by the peculiarities of the particular profile from which the sample

![Figure 5](image-url)
was taken, the moisture equivalent seemed to be a more suitable basis for a generalized comparison than the field capacity. It should be noted, however, that below a moisture equivalent of about 5 the discrepancy between the moisture equivalent and field capacity increases sharply; according to Browning (7), in soils of very coarse texture the field capacity may be two or more times the moisture equivalent. This, doubtless, accounts for the apparently high proportion of the available moisture held in the wilting range of the four soils of lowest moisture equivalent (fig. 5). Most soils of importance in agriculture fall within the textural range corresponding to moisture equivalents of 5 to 45, and in this range the proportion of the available moisture in the wilting range varies from about 11 to about 30 percent, averaging roughly 20 percent. It is clear that the proportion of the total available moisture that is held in the wilting range is great enough in most soils to be of significance in any consideration of the influence of soil-moisture shortage on the behavior of plants.

While it is not supposed that there is a sharply defined transition in the properties of the soil water or in the mechanism of water absorption by the plant at the first permanent wilting point or the ultimate wilting point, it seems possible to make a fairly well-defined division of soil moisture, so far as its availability to plants is concerned, into (1) that available for vegetative growth, (2) that available for maintenance of life under conditions of greatly reduced turgor, and (3) that unavailable to plants.

Because of the time and labor involved in making direct determinations of the wilting point of soils, several investigators have proposed less laborious, indirect methods, based upon physical measurements and not involving the growing of plants in the soil. The most widely used of these methods, that of Briggs and Shantz (6), is based upon an expected constancy of the ratio of the moisture equivalent to the first permanent wilting point, which they found to be approximately 1.84 in about 28 soil types investigated. Veihmeyer and Hendrickson (15) and, later, others called attention to the fact that in many soils the ratio of moisture equivalent to wilting point deviates widely from the value 1.84, observed by Briggs and Shantz.

Since the ratios reported by some workers (15) were nearly all above 1.84 and those reported by others (16) were nearly all below 1.84, it seemed possible that some of the variations in ratio observed may have resulted from variation in the degree of wilting judged by the different workers to be permanent wilting. In the present investigation, since the entire wilting range was determined, the possible importance of this factor may be evaluated from the data shown in figure 4. It is apparent from these data that wide variation in degree of permanent wilting could cause appreciable variation in the ratio of moisture equivalent to wilting point; but even the widest variation in this respect could account for only a part of the observed variability in ratio of these soils, since the ultimate wilting point of some lies far above the first permanent wilting point of others of about the same moisture equivalent. These data fully confirm the conclusion of Veihmeyer and Hendrickson (15) and others, that the ratio of the moisture equivalent to the wilting point of different soils varies widely. At first permanent wilt the moisture content of soils within the narrow
moisture-equivalent range of 30 to 31 varied from 7.6 to 20.2 percent and the ratio of the moisture equivalent to the first permanent wilting point varied from 3.97 to 1.53. The highest ratio of the moisture equivalent to the first permanent wilting point obtained in any of the soils (3.97) was obtained with a sample classified as Coachella fine sand, though it had moisture equivalent of 30.2 and mechanical analysis showed 30 percent silt and 40 percent colloid; whereas the lowest ratio, 1.08, was obtained with a coarse sand that had a moisture equivalent of 1.3 and was probably very low in percentage of colloid.

In an investigation of the relation of soil-moisture properties to texture in a large number of soils of the Okanagan Valley, British Columbia, Wilcox and Spilsbury (20) found that the values obtained for the wilting coefficient by the cohesion method of Bouyoucos (5) were closely correlated with the percentages of colloid as determined

![Graph showing the relation between percentage of soil colloids and first permanent wilting point of different soils.](image)

**Figure 6.**—Relation between percentage of soil colloids and first permanent wilting point of different soils.

by the hydrometer method of Bouyoucos (4). They concluded that the wilting coefficient may be calculated from the equation

\[
\text{Wilting coefficient} = 0.12 \text{ percent colloid} + 1.338
\]

with only a relatively small amount of error, though they warn that this equation may not prove satisfactory for use with soils formed under climatic conditions differing widely from those of the Okanagan Valley.

The relation of the first permanent wilting point to the percentage of colloids, as determined by the hydrometer method, unveils that most of the soils used in the present investigation, is shown in figure 6. It is obvious that the relation is not constant. For the 71 soils the average

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*Thanks are due Dr. Walter Reuther, of the U. S. Date Garden, Indio, Calif., and James A. Cook, formerly of that garden, for the mechanical analysis of these soils.*
ratio of percentage of colloids to first permanent wilting point was 3.21, but the ratios ranged from 1.85 to 5.29.

Although, in a general sense, with increasing fineness of texture there is an increase in the moisture equivalent, the percentage of colloids, and the wilting range, it is apparent that there are differences in the physical make-up of these soils that are not reflected in the moisture equivalent or the percentage of colloids.

A striking illustration of the failure of the moisture equivalent or percentage of colloids to reflect accurately the moisture-holding properties of the soil is that of several samples of soil from recent alluvial formations in the Coachella Valley, Calif. These soils are composed of 26 to 29 percent sand, 29 to 38 percent silt, and 32 to 45 percent colloids. The values for the first permanent wilting point range from 7.6 to 8.9 percent and for the moisture equivalent from 30.2 to 30.6 percent. It appears that, in relation to either the moisture equivalent or the percentage of colloids, these soils hold exceptionally low amounts of water at the first permanent wilting point.

It is possible that the movement of water through the soil to root surfaces, the number or distribution of roots, or perhaps the operation of other factors that might affect the value of the wilting points is related to variations in the texture and structure of the soil and in the composition of the soil solution; but it is highly probable that a large part of the variation in the ratios of the moisture equivalent or the percentage of colloids to the first permanent wilting point can be attributed to variations in the relative amounts of water retained by different soils with variations in soil-moisture tension. For example, the statement previously made regarding the moisture-holding properties of the Coachella Valley soils, as compared with others of similar moisture equivalent or percentage of colloids, may be generalized as follows: Soils A and B retain about the same amount of water at low moisture tension (moisture equivalent), while at high tension (wilting range) soil A retains less water than soil B.

Olmstead (12) found pronounced variations in the relative amounts of water retained by soils that had been saturated and then centrifuged in fields of 1,000 and 300,000 gravity, and more recently Richards and Weaver (14), using their porous-plate and pressure-membrane apparatus, found that the relative amounts of moisture retained by soils may vary over the entire range of moisture tensions from that at field capacity to that at the ultimate wilting point. Their curves showing the moisture retained by different soils at tensions ranging from about 2 to about 20,000 cm. of water are, however, more nearly parallel in the tension range above 3,000 cm. of water than in the range below this value. In their investigation, Richards and Weaver used duplicate samples of most of the soils employed in the present study. Their comparisons of the moisture percentage of these soils at a moisture tension equivalent to 15 atmospheres with the moisture percentages at the two wilting points suggest that the relation of the first permanent wilting point or of the ultimate wilting point to the 15-atmosphere percentage is more nearly constant than the relation of either of the wilting points to the moisture equivalent or to the percentage of colloids. The 15-atmosphere percentage would, therefore, probably serve as a more reliable basis for the indirect determination of the wilting range than would the moisture equivalent or the percentage of colloids.
DISCUSSION AND CONCLUSIONS

The idea that a soil has a relatively definite wilting coefficient, or first permanent wilting point, has been seriously questioned by various writers from time to time since Briggs and Shantz (6) first published the results of their work on this subject. Questions as to the reality of a first permanent wilting point have been raised, possibly as a result of a misunderstanding of (1) the meaning of the term “first permanent wilting point,” (2) the precautions essential for the reliable determination of its value, and (3) the use to which it may be put in interpreting the behavior of plants in relation to soil-moisture conditions in the field.

The first permanent wilting point might be defined as that percentage of soil moisture at which the forces acting on the water in the soil are at approximate equilibrium with the forces acting on the water in a plant which is at that stage of turgor at which vegetative growth practically ceases. At moisture percentages above the first permanent wilting point, temporary wilting, or even death of much of the leaf surface, may result from prolonged exposure to conditions that produce intense transpiration. As long, however, as the moisture content of the soil is above the first permanent wilting point, vegetative growth of the plant may be resumed if transpiration is reduced to a negligible rate and other conditions are kept favorable for growth.

The results of the investigations of Caldwell (8) and of Shiye and Livingston (16) have frequently been cited as proof that the moisture content of the soil at which permanent wilting takes place is affected by the environmental conditions existing during the wilting process. In the course of the present work, however, it was demonstrated many times that wilting plants rapidly or slowly made no significant difference in the soil-moisture percentage at first permanent wilt, provided the plants were placed in a humid chamber before the basal leaves were injured and before the second pair of leaves was permanently wilted. In the present investigation the plants were protected from rapid water loss after the first one or two temporary wiltings, because it was found that under conditions of low transpiration fewer transfers back and forth from the greenhouse bench to the humid chamber were required than if the plants were subjected to intense water loss. It seems possible that in reported instances of appreciable influence of the environment during wilting on the moisture content of the soil at permanent wilting the leaves may have been injured before the plants were placed in the humid chamber, that the degree of wilting may have been allowed to go beyond that of first permanent wilting before the plants were placed in the humid chamber, or that the roots may have been injured by high soil temperatures. Caldwell (8) reported root injury, which he attributed to desiccation, in some of his cultures. In the present work root injury, apparently resulting from high soil temperatures caused by exposure of several culture cans to direct sunlight on a hot day, was observed when the cultures were at soil-moisture percentages above the first permanent wilting point. Root injury that could be attributed to desiccation alone, however, was never observed in cultures dismantled
at the first permanent wilting point; and even at the ultimate wilting point most of the root system appeared to be alive.

The reality of a first permanent wilting point (wilting coefficient) of the soil has been questioned by some writers because soil-moisture conditions and wilting often appear not to be very closely related in the field. Soil within the root zone of plants in the field may be found to vary in moisture content from percentages well above the first permanent wilting point to percentages well below it; at the same time, depending upon the species and the weather conditions, some plants may show severe wilting and others no visible signs of water shortage. Wilting of a normal uninjured plant when the soil in the entire root zone is above the first permanent wilting point is temporary, and the plant may recover turgor and continue vegetative growth when transpiration becomes sufficiently reduced. On the other hand, it is not unusual to find under field conditions that the moisture content of the soil in a part of the root zone is below the first permanent wilting point before permanent wilting occurs and vegetative growth ceases. When temporary wilting occurs or a comparable state of turgor is reached in plants that do not show wilting, the diffusion-pressure deficit of the roots may soon become great enough to make possible absorption of water from soil at moisture percentages below the first permanent wilting point. This is likely to occur only in the zones of highest root concentration, while the soil in zones of lower root concentration is still above the first permanent wilting point. Then, when transpiration is greatly reduced, as at night, the plant may recover sufficient turgor, as a result of water absorbed by roots in soil at moisture percentages above the first permanent wilting point, to resume vegetative growth.

A prerequisite to the rational application of the conception of a wilting range of the soil to field conditions is an understanding of the manner and pattern of water extraction by the plant from the soil. From extensive field work relating to irrigation problems, there has been formulated the following picture of the typical pattern of root distribution and the sequence of events in the extraction of water from soil initially wet to soil at the ultimate wilting point. While the distribution of roots varies greatly with species and soil, the concentration of absorbing roots is typically greatest in the upper part of the root zone and near the base of the plant and decreases with soil depth or distance from the plant. Extraction of water is most rapid in zones of highest root concentration and most favorable conditions of temperature, aeration, and other environmental factors. When the moisture content in the zone of highest root concentration has been reduced to the first permanent wilting point, extraction in this zone does not cease, but the rate falls off sharply and the total water absorption rate of the plant decreases. As the total absorption rate and the turgor of the plant decrease, the diffusion-pressure deficit of the root system as a whole increases, the soil-moisture percentage is lowered into the wilting range progressively in zones of lower and lower root concentration, and, finally, as the severity of wilting increases, the soil-moisture percentage is reduced to the ultimate wilting point progressively from zones of highest root concentration to zones
of lower root concentration. By the time the plant in the field dies as a result of desiccation, the soil-moisture percentage in a large part of the root zone may have been reduced to the ultimate wilting point. Soil at the extremities of the root system, however, may still be well above the first permanent wilting point. The plant dies, not because water absorption has absolutely ceased, but because the rate of absorption finally lags too far behind the rate of loss to support life.

The significance of the first permanent wilting point or of the ultimate wilting point in the interpretation of field data lies in the fact that these points serve as reference values to which soil-moisture percentages may be related in making estimates of the amount of water in the root zone of a plant that is available for vegetative growth or for the maintenance of life.

It is hardly to be hoped that plant responses to soil-moisture conditions in the field may be very sharply defined. By the time the plant shows any visible effect of moisture shortage the moisture content of the soil in different parts of the root zone may vary widely; and atmospheric conditions, depth and distribution of roots, nutrition of the plant, the differences in susceptibility of different species to injury by temporary desiccation, and doubtless other factors affect the response of the plant in the field to soil-moisture conditions. By actual experiment with a given species of plant and set of soil conditions, however, it is possible to predict with a fair degree of accuracy the response that a plant will make when the moisture content of the soil in various proportions of the root zone is reduced to percentages in the wilting range under similar conditions of soil and climate.

SUMMARY

The range of soil-moisture percentages through which plants undergo permanent wilting has been termed the "wilting range of the soil." If the sunflower is used as the test plant, the upper end of this range, the first permanent wilting point, is marked by permanent wilting of the basal leaves, and the lower end of the range, the ultimate wilting point, is marked by complete permanent wilting of the apical leaves.

A standardized procedure for making wilting-range determinations is described, and the results obtained on about 80 soils are presented. At soil-moisture percentages near or in the wilting range even a low rate of water loss from the plant had an appreciable effect upon the osmotic pressure of the sap and upon the turgor of the plant. A decrease in soil moisture from field capacity to the first permanent wilting point caused, in plants in dry air, an increase of 5 atmospheres in the osmotic pressure of the sap and, in plants in humid air, an increase of only 2.5 atmospheres. The changes in osmotic pressure of plants in humid air indicate that the diffusion-pressure deficit of the plant was somewhat less than 9 atmospheres at the first permanent wilting point and about 22 atmospheres at the ultimate wilting point.

The proportion of the available moisture in the wilting range is great enough to be of considerable significance in investigations of the effect of soil-moisture shortage on plants. Of the moisture held between the ultimate wilting point and the moisture equivalent, the
proportion held within the wilting range of the soils investigated varied from about 11 percent to about 30 percent and averaged about 20 percent.

It was found, in agreement with other work, that the ratio of the moisture equivalent to the first permanent wilting point or to the ultimate wilting point is not constant. It was also found that the percentage of soil colloids, which has recently been used as a basis for calculation of the wilting point, would not serve as a reliable basis for calculation of the wilting points of the soils used in this study.

As related to plant behavior, soil moisture may be classified as (1) moisture available for vegetative growth, (2) moisture in the wilting range, and (3) moisture unavailable to plants.

In field work the first permanent wilting point and the ultimate wilting point may be used as reference values for estimating, respectively, (1) the amount of moisture in a soil that is available for vegetative growth and (2) the amount available for mere maintenance of life.

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