SOME WATER RELATIONS OF THREE WESTERN GRASSES. II. DROUGHT RESISTANCE. III. ROOT DEVELOPMENTS [1]

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THIS PAPER is the second of the series in which the water relations of some grasses suitable for use in soil-conservation projects in semiarid regions is considered. In the first paper (Bailey, 1940) the transpiration ratios of *Agropyron Smithii* Rydb., *A. ciliare* (Trin.) Franch., and *Bromus marginatus* Nees. were reported. It was pointed out there that plants useful for soil conservation in dry-land habitats must be adapted to binding soil, that they must be physiologically suited to withstand periods of drought without excessive injury, and that it is desirable that they should be economical in their use of the limited supply of moisture. The transpiration ratio was used as an expression of the relative water utilization of the three grasses. In the present study the abilities of the same species of plants to withstand drought conditions are considered, as well as the character and extent of their root systems.

II. DROUGHT RESISTANCE.—Frequently it is assumed that the transpiration ratio is an indication of the degree of drought resistance of plants; however, this is not always true. Maximov (1923) found that some xerophytes have higher transpiration ratios than certain mesophytes. Several investigators have found that drought-resistant hybrids and varieties of crop plants demonstrate no special efficiency in the use of water (Briggs and Shantz, 1913; Kiesselbach, 1916; Dillman, 1931). Thus, the transpiration ratio cannot be considered as a criterion of drought resistance.

Plants such as the three grasses used in the present study exhibit two degrees of response to drought, depending on the severity and duration of the dry conditions. If the period of drought is short, the grasses may become severely wilted, but they will recover immediately upon the resumption of favorable moisture conditions. Prolonged drought, however, may cause the aerial portions of the plants to die and the subterranean portions to become dormant. When water is again available, new shoots will be sent up, and the plants will resume growth; but a certain amount of injury to the plants occurs. In this study an effort has been made to analyze both of these aspects of drought resistance.

Drought resistance as measured by the water balance.—Maximov (1929, 1931) considers that physiologically the chief adaptation of drought-resistant xerophytes is their ability to withstand large losses of water from the protoplasts without injury and that the extent of this dehydration at the time when injury ensues serves as a measure of the relative xerophytism of such plants. Maximov and Krasnosselsky-Maximov (1924) have shown that the amount of water retained by different types of plants at the time of wilting is inversely related to the aridity of their natural habitats. Henrici (1926) found that certain xerophytic grasses could lose as much as 50 per cent of the fresh weight of their foliage without injury.

When transpiration from a plant exceeds the absorption of water, it becomes wilted. A plant is "permanently wilted" when it does not recover after twenty-four hours in a saturated atmosphere, without the addition of water to the soil (Briggs and Shantz, 1912). The amount of water that a plant has lost on the incidence of permanent wilting, expressed as percentage of its water content when turgid, is known as the "water balance" (Paltridge and Mair, 1936). The amount of water retained by a plant at permanent wilting, expressed as percentage of its water content when turgid, is known as the "water residuum" (Paltridge and Mair, 1936). The water balance plus the water residuum equals one hundred.

If, as Maximov proposes, the water balance of a plant is an expression of its xerophytism, it should be possible to utilize this criterion to measure the drought resistance of plants. In its simplest form such a procedure would involve allowing plants to reach the stage of permanent wilting and comparing their water contents with those of similar plants which had been kept turgid. The water balance, obtained in this manner, would be an expression of the xerophytism. A high water balance should indicate the ability to withstand drought, since a large reduction in the water content could occur before injury to the plant ensued.

The principle difficulty in such a procedure would be the accurate determination of the stage of permanent wilting. In many plants, such as most dicotyledonous species, this stage of wilting can be ascertained with a considerable degree of certainty from the appearance of the plants; however, grasses and other monocotyledonous plants have no definite demarcation of the onset of permanent wilting. In the latter case, other means of detecting permanent wilting are necessary.

Bakke (1915), using the cobalt-chloride paper method, studied the transpirational behavior of uprooted sunflower plants. He found that transpiration decreased very rapidly the first hour and then progressively less for the next four hours until the rate was almost constant. After the fifth hour a marked increase in transpiration occurred which lasted for

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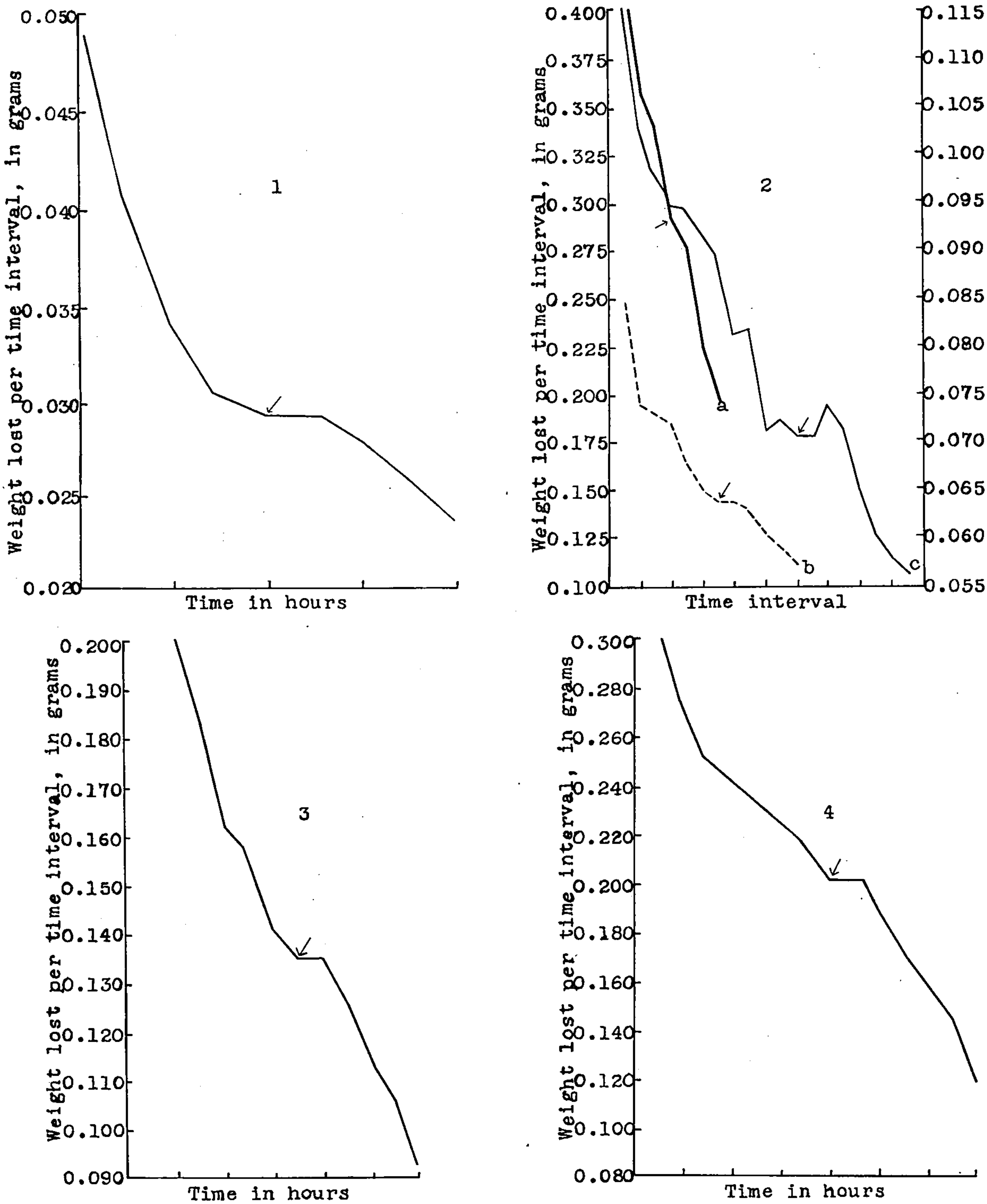

Fig. 1–4.—Fig. 1. Curve illustrating the transpirational behavior of an uprooted plant of *Themeda australis*. The arrow indicates the critical level of dehydration. The water balance was 28.2 per cent. After Paltridge and Mair (1936).—Fig. 2. Curves illustrating the transpirational behavior of an uprooted *Agropyron Smithii* plant. Curve *a* is for hourly intervals; curve *b* is for half-hourly intervals; curve *c* is for quarter-hourly intervals. Curve *c* is plotted with the scale on the right ordinate axis. The arrows indicate permanent wilting at the corresponding points on the three curves. The water balance was 41.5 per cent.—Fig. 3. Curve illustrating the transpirational behavior of an uprooted *Agropyron ciliare* plant. The arrow indicates the critical level of dehydration. The water balance was 50.8 per cent.—Fig. 4. Curve illustrating the transpirational behavior of an uprooted *Bromus marginatus* plant. The arrow indicates the critical level of dehydration. The water balance was 52.8 per cent.

two hours, after which the rate again decreased steadily until the plants became dry. Bakke attributed the sharp increase in the transpiration rate after the fifth hour to a rupture of the water columns within the plant and a consequent release of internal tensions. He considered this rupture of water columns to indicate the onset of permanent wilting. This method of indicating permanent wilting is satisfactory but it requires considerable skill in practice. The use of cobalt-chloride paper on the narrow, inrolling leaves of grasses is particularly difficult.

Paltridge and Mair (1936) found that the sharp change in the rate of transpiration at permanent wilting noted by Bakke could also be observed by weighing. In this method, uprooted plants were weighed at regular intervals, the difference calculated from any two consecutive weighings being a measure of the average rate of water loss from the plant during that time interval. As in the case of the cobalt-chloride paper method, the rate of transpiration decreased steadily with time up to a certain point. At this stage the gradual deceleration halted for a time, later to be resumed until the plants were dry. The results for *Themeda australis,* as obtained by Paltridge and Mair, are presented in graphical form in figure 1. These investigators were not able to observe any rise in the rate of transpiration as Bakke had done. In their investigation the halt in the deceleration was evidenced not by an increase in the transpiration rate, but by the persistence of a constant rate for a period of one or two hours. A study of this discrepancy in the two methods of determining permanent wilting led Paltridge and Mair to the conclusion that, in reality, the critical moisture content was indicated with Bakke's method by the period of constant transpiration rate that preceded the acceleration period.

Paltridge and Mair found that the water residuum in any one species of grass is almost constant for plants up to twelve months after germination. There is, however, a very marked difference in the time elapsing before the water contents of young and old plants reach the critical level.

These investigators also studied the effect of different environmental conditions, existing during the growth period of the plants, upon the magnitude of their water balance. Plants of *Themeda australis,* grown under widely-differing meteorological conditions, gave similar values for the water balance. No appreciable effect of different levels of soil moisture upon the water balance was obtained; however, for plants grown in very wet soils, the temporary halt in the deceleration of transpiration was of short duration and hardly distinguishable even in the quarter-hourly readings.

The experiments reported here were modeled after the technique developed by Paltridge and Mair, with certain modifications.

Plants were grown in four-inch flower pots in the greenhouse. They were thoroughly watered 36 to 48 hours before the experiment, after which no more water was added. The plants were placed under a bell jar twelve hours before readings were begun. At the close of this period they were taken from the pots and all soil carefully removed. Best results were obtained if no water was used in this process. After some practice, the process of freeing the roots from soil could be accomplished in less than five minutes. It was thought that plants grown in sand could be cleaned most readily; however, the grasses used in this investigation did not grow satisfactorily in sand.

When the plants were free of soil, they were immediately tied to one arm of an analytical balance and the weight obtained. Thereafter they were weighed at fifteen-minute intervals. During the first few minutes after removal from the soil, grasses lose water very rapidly; consequently, an appreciable loss of weight occurs during the period of cleaning. In order to obtain an estimate of this unmeasured water-loss, the plants were weighed at five-minute intervals during the first quarter hour and the loss during the five minutes prior to the first weighing was calculated as two-thirds of the total loss occurring during the ensuing ten minutes. Paltridge and Mair found that an error of as much as 200 per cent in thus estimating the loss of water during the first five minutes of an experiment would not appreciably affect measurements of the water balance of plants.

The weight of the plant at the end of each fifteen-minute interval was recorded in tabular form. By subtracting each weight from the one just preceding, the loss of water for each fifteen minutes was ascertained. The summation of two or four of these quarter-hourly losses gave the transpiration for periods of thirty minutes and one hour. At the conclusion of the weighing, the plants were dried to constant weight in an oven at 98° to 100°C., and the original green weight was calculated. The water residuum at the critical stage of wilting was then determined, and the water balance was obtained by subtracting the water residuum from one hundred.

After the data for each plant were completely tabulated, they were recorded graphically in the manner shown in figure 3. The critical level of wilting is readily recognized on such a curve.

The general practice was adopted of plotting the water losses for each time interval tabulated—i.e., quarter-hourly, half-hourly, and hourly intervals (fig. 2). Not all of these curves show clearly the critical level of wilting. In figure 2, the curve based on hourly periods gives no indication of the halt in deceleration of transpiration, whereas the curve for fifteen-minute intervals has several irregularities which could be interpreted as indications of the halt in deceleration. The curve of thirty-minute periods of water loss shows clearly the onset of permanent wilting. The length of the halt in the deceleration of transpiration is determined by the size of the particular plant used in the experiment. For the most part, the critical level of wilting was evidenced most distinctly in these experiments on the curve representing thirty-minute intervals.

It is obvious that the greatest accuracy in determining the stage at which permanent wilting is initiated is obtained by using the curve for the shortest time interval, providing this curve can be accurately interpreted. Paltridge and Mair (1936), however, found that the error resulting from the use of the curve for hourly periods was only 5 per cent, so that it is permissible to use the simpler method of plotting graphs on the basis of the longest time intervals which will give a clear indication of permanent wilting.

Each of the three grasses used in these experiments has been analyzed with respect to the magnitude of its water balance. Twenty tests each were made for *Agropyron Smithii* and *Bromus marginatus,* and ten tests were made for *Agropyron ciliare.* Figures 2, 3, and 4 show typical curves for the three species. In each of these graphs the loss of water for each time interval is plotted on the ordinate axis, and the time intervals are shown on the axis of the abscissa. An arrow indicates the stage at which permanent wilting ensues. The water balance is determined by subtracting the water residuum at this stage from one hundred.

The average water balance for each of the three species of grasses follows. The standard error accompanies each mean. *Agropyron Smithii,* 41.6 ± 1; *Bromus marginatus,* 49.1 ± 1; *Agropyron ciliare,* 50.3 ± 1.2.

Agropyron Smithii has the lowest water balance and, consequently, is able to endure less dehydration without injury than the other two species.

Drought resistance resulting from the ability of underground parts of the plant to remain dormant.—In the Plains region of the United States drought conditions are severe enough occasionally to cause the foliage of native plants to die. Under such circumstances the roots of many plants succumb. However, the underground parts of certain types of plants are capable of becoming dormant and remaining in this condition for long periods of time. Upon the advent of favorable growth conditions the latter type of plants resumes growth and sends up new shoots. Although such plants suffer a certain amount of injury, they are, nevertheless, drought resistant. They are the first plants to appear above the ground after an extremely severe drought period.

Apparently, the relationship of this type of drought resistance to that characterized by the ability of the plant to withstand dehydration of foliage without injury has not been investigated.

In these experiments an effort was made to determine the relative drought resistance of *Agropyron Smithii, A. ciliare,* and *Bromus marginatus,* as evidenced by their ability to recover after a period of severe drought. In 1938 each species was planted in eight metal pots containing greenhouse soil. The capacity of these pots was about 7 kg. of oven-dry soil. For a period of about six weeks the soil moisture was maintained at 25 per cent of the dry weight of the soil in these potometers. During this time all the plants grew vigorously and became firmly established.

Following this period of active growth soil moisture was reduced to 10 per cent of the dry weight of the soil. The wilting coefficient for this soil was 16.2 per cent. The plants were kept in this condition for six weeks, during which time the foliage died. At the end of this period water was added to each potometer. Within ten days every plant was growing vigorously. The plants were then placed in a dry compartment of a greenhouse, and the soil in the pots was brought to air-dryness (approximately 4 per cent of the dry weight of the soil). This condition was maintained for five months, during which time no water was added to the pots. Again the tops became completely dry, and the underground parts of the plants became dormant.

This second drought was terminated by adding a liter of water to each pot. Within two weeks every one of the twenty-four plants recovered. Several new shoots were present on each plant of *Agropyron ciliare* and *A. Smithii.* In the latter case many of the new shoots were produced around the edges of the pots from rhizomes. Two plants of *Bromus marginatus* produced only three new shoots; however, the plants in the other six pots produced many new shoots.

Again the soil in each pot was allowed to reach the air-dry condition. This third period of drought was terminated after six months. At this time drought conditions had prevailed for approximately one year. None of the plants of *Agropyron ciliare* and *Bromus marginatus* responded to the addition of water; however, one-half of the plants of *Agropyron Smithii* resumed growth, although this growth was not vigorous.

Discussion.—The evaluation of the drought resistance of grasses involves the consideration of two factors—viz., their ability to withstand dehydration without injury and the ability of their underground parts to remain dormant during periods of drought. Paltridge and Mair (1936), in their extensive study of the first of these two factors, have classified seventeen grasses on the basis of their water balances as follows:

- Mesophytes.—Plants having a water balance less than 50 per cent.
  - True mesophytes.—Water balance less than 25 per cent.
  - Xerophytic mesophytes.—Water balance, 25–50 per cent.
- Xerophytes.—Plants having a water balance more than 50 per cent.
  - Mesophytic xerophytes.—Water balance, 50–75 per cent.
  - True xerophytes.—Water balance more than 75 per cent.

These investigators found that the relative xerophytism of the different grasses, as determined in their experiments, was in accordance with the relative aridity of their natural habitats.

On the basis of this classification the three grasses used in the present study are xerophytic mesophytes. *Agropyron Smithii* is the most mesophytic, with a water balance of 41.6 ± 1. *Agropyron ciliare* and *Bromus marginatus,* having water balances of 50.3 ± 1.2 and 49.1 ± 1, respectively, are considerably more xerophytic. These values for the water balance do not indicate marked ability to withstand drought.

Paltridge and Mair included a few plants common to the United States in their study. These plants, with their water balances (as read from diagrammatic representations), were: *Lolium perenne* L., 33; *Festuca rubra* L., 48; *Agropyron cristatum* Gaertn., 80; *Polygonum aviculare* L., 43; *Plantago lanceolata* L., 38.

Agropyron ciliare and *Bromus marginatus* have water balances similar to that of *Festuca rubra.* All three of these grasses are adapted to moderate moisture conditions. *Agropyron Smithii* and *Polygonum aviculare* have similar water balances and require somewhat more moisture than the species just mentioned. The water balance of *Agropyron cristatum,* determined by Paltridge and Mair, was much higher than the figures obtained in this investigation for the three species of grasses used. This is in accordance with the relative aridity of the natural habitats for each of these four grasses.

The ability to remain dormant during long periods of drought is very important to survival of plants in arid regions. Although the three grasses used in this study do not show a marked degree of xerophytism as evidenced by dehydration of uprooted plants, they are, nevertheless, able to survive drought in a dormant condition to a rather remarkable extent. *Agropyron Smithii* was especially notable in this respect, since it recovered after a drought period of twelve months' duration. This type of drought resistance, combined with the ability to grow rapidly, accounts for the fact that after severe droughts this grass frequently dominates areas on which it previously had formed only a small part of the vegetational cover (Weaver and Albertson, 1936; Judd, 1937).

III. Root development.—It is well known that, as a group, grasses are effective in stabilizing soil masses. Their roots are shallow, closely matted, and widespreading; frequently rhizomes or stolons are present. It remains to determine which species of grasses will bind soil most efficiently.

In the first paper of this series (Bailey, 1940), it was shown that the three grasses used in these investigations produce about 50 per cent of their total growth as roots. In the case of *Agropyron Smithii* the inclusion of rhizomes with the roots brought the quantity of underground parts of the plants to more than 60 per cent of the total growth. This extensive development of subterranean portions of the plants is of considerable importance from the standpoint of soil binding.

In addition to the quantity, the depth and lateral spread of the roots are important factors in determining the usefulness of plants for soil-conservation purposes, especially in the dry regions of the western part of the United States. A deeply-rooted plant obtains moisture stored at considerable depths in the soil and is consequently protected to a certain extent against drought injury. A widespreading development of surface roots is desirable in soil-conserving plants, since a large area of soil can be stabilized by each plant.

Agropyron Smithii has been found to extend roots to a depth of four to eight feet (Weaver, 1926; Judd, 1937). Spence (1937) describes the root system of *Bromus marginatus* as being concentrated in the

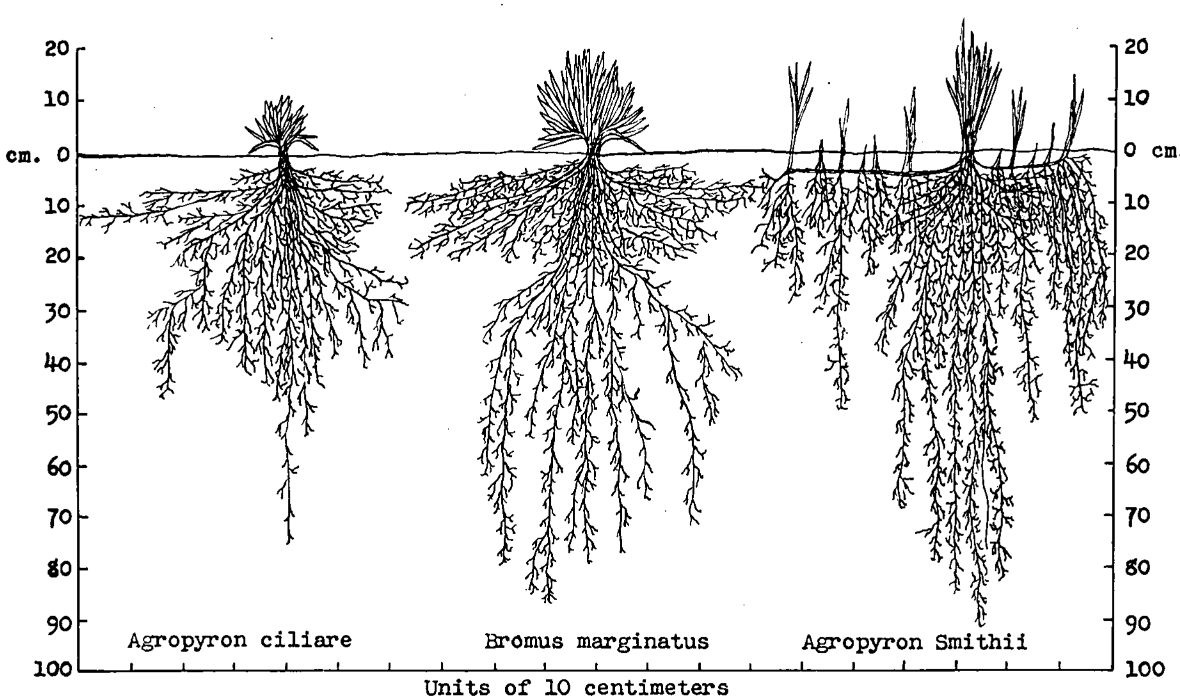

Fig. 5. Bisect showing underground parts of *Agropyron ciliare, Bromus marginatus,* and *Agropyron Smithii.* Only those roots occurring in a four-inch vertical section of soil are shown.

upper 3 centimeters of soil, with many roots occurring in the upper 40 centimeters.

In this study plants of *Agropyron Smithii, A. ciliare,* and *Bromus marginatus* were grown in the field in an area from which all other vegetation was removed. No other plants were allowed to become established in the area during the entire growing season. The soil in which these grasses grew was a dark loam with many pebbles to a depth of ten inches. From ten to thirty inches a gravelly gray clay occurred which had numerous spots of iron accumulation. Below thirty inches was the tan, sandy subsoil. All plants of each species grew exceptionally well, the rhizomes of *Agropyron Smithii* extending as much as forty centimeters from the main clump.

At the end of the growing season a trench four feet in depth and three and one-half feet in width was dug beside each plant. Each trench was so situated that one wall was about four inches from the base of the plant. This wall was dug out with an ice pick until it was even with the plant. The roots were carefully freed from the soil as they were encountered. A bisect of the root systems of the grasses was obtained in this manner, a four-inch layer of roots being included in the bisect. The position of each root was charted as soon as it was exposed.

Root charts for each of the three species are shown in figure 5. It is not supposed that the bisects show the maximum spread and depth of roots for these species, since the plants grew in the field for only eighty days prior to their excavation; however, the general nature of the root systems are shown.

Each of the three grasses had a large percentage of its roots in the upper twenty centimeters of soil. *Agropyron Smithii* was particularly well developed in this respect, since many roots were associated with the rhizomes produced. *Bromus marginatus* produced surface roots almost as abundantly as *Agropyron Smithii.* The roots of *Agropyron ciliare* were poorly developed in this respect. The root-spread for *Agropyron Smithii* was 72 centimeters, as compared to 70 centimeters for *Bromus marginatus* and 64 centimeters for *A. ciliare.* From the standpoint of soil binding *Agropyron Smithii* appears to be the most desirable of the three species, as evidenced by the quantity and extent of the surface roots.

The depths of the roots of *Agropyron Smithii* and *Bromus marginatus* were approximately the same, about 90 centimeters. The roots of *Agropyron ciliare* extended downward 70 centimeters.

The ability to withstand drought is frequently associated with deep rooting and the consequent absorption of water from the soil at considerable depths. At least two of these species, *Agropyron Smithii* and *Bromus marginatus,* have roots that penetrate to sufficient depths in the soil to enable them to withstand drought to a considerable extent.

SUMMARY

The drought resistance of *Agropyron Smithii, A. ciliare,* and *Bromus marginatus* is considered from two standpoints—viz., their ability to withstand dehydration without injury and the ability of their underground parts to reman dormant during periods of drought. *Agropyron Smithii* loses 41.6±1 per cent of its total water content before permanent wilting ensues. *Bromus marginatus* and *Agropyron ciliare* lose 49.1±1 and 50.3±1.2 per cent, respectively, of their total water contents before the onset of permanent wilting. These values indicate only a moderate ability to withstand drought without injury.

The subterranean parts of all three species remained dormant during a period of six months of severe drought, and produced new shoots when water was added to the soil. After another drought period of six months' duration, only *Agropyron Smithii* resumed growth when water was added to the pots.

Root bisects of field plants of the three grasses revealed that a large percentange of the roots of each species occurred in the upper twenty centimeters of the soil. From the standpoint of the percentage of surface roots, the spread of surface roots, and the depth of rooting, *Agropyron Smithii* is the most desirable species for soil-conservation purposes.

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PHYSIOLOGIC RACES OF OAT SMUTS [1]

George M. Reed

THE EXISTENCE of specialized races of oat smuts was first demonstrated by Reed in 1924. Collections of *Ustilago levis* (Kell. and Sw.) Magn. from Columbia, Missouri, and Aberystwyth, Wales, gave different results on *Avena brevis* Roth and certain varieties of *A. sativa* L. The Welsh smut infected *A. brevis,* giving practically negative results on several varieties of *A. sativa.* The Missouri smut infected some varieties of *A. sativa* and *A. brevis* only slightly. Both smuts severely infected some varieties of *A. strigosa* Schreb. A collection of *U. avenae* (Pers.) Jens. from Missouri infected Hull-less and varieties of *A. strigosa,* while the Welsh collection did not. A few varieties of *A. sativa* were infected by both collections, others remaining free. These results were confirmed by Sampson in 1925.

Reed (1927) reported the occurrence of two distinct specialized races of the loose smut on the red oats, one on strains of Fulghum and the other on Red Rustproof. Reed (1929) described 11 races of loose smut and 5 of covered on the basis of their behavior on various oat species and varieties, the smut collections having been obtained from widely separated regions. Reed and Stanton (1932) published additional data on the smuts of the red-oat group, describing a specialized race of the covered smut on Fulghum. Reed (1932) found that Black Mesdag, hitherto a recognized resistant variety of oats, was susceptible to the Fulghum covered smut. Reed and Stanton (1936) published data indicating that there was more than one race of covered smut on the Fulghum varieties. Sampson (1929) described a race of loose smut on *A. brevis* in Wales. For Germany, Nicolaisen (1931) recorded the occurrence of several races of loose smut on oat varieties, and Schattenberg (1934) gave further data on the specialization of this species. Radulescu (1935) described four races of loose smut in Rumania. Roemer, Fuchs, and Isenbeck (1937) announced the existence of a special race of loose smut which attacked Black Mesdag, and Vaughan (1938) reported that two collections, one from Kansas and one from Oklahoma, produced high infections on this variety.

The primary basis for the evidence of physiologic specialization is the behavior of the different collections of the smuts on the particular strains of oat varieties. Some strains may be infected by one collection and not by others, and one of the problems involved is the selection of suitable hosts for the differentiation of the specialized smut races. There are a large number of varieties and strains belonging to the recognized species of *Avena* that are available for making the necessary tests.

Bartholomew and Jones (1923) and Reed and Faris (1924) demonstrated that successful infection of susceptible oats by both loose and covered smuts is dependent upon the environment. Inoculated seed planted directly in the soil usually gives variable results, with a low percentage of infection. Extensive experiments have demonstrated that the removal of the hulls from the grains, inoculation with the dry smut spores, and then germination of the seed at a temperature of 20°C. in soil or sand with a low water moisture, give high percentages of infection. This procedure was followed in the present studies.

Approximately 200 varieties and strains, belonging to nine species of *Avena*—*Avena barbata* Brot., *A. brevis* Roth, *A. byzantina* C. Koch, *A. fatua* L., *A. nuda* L., *A. nudibrevis* Vav., *A. sativa orientalis* (Schreb.) Alefeld, *A. sativa* L., *A. strigosa* Schreb. —have been used in the course of the experiments. Many of these reacted in a similar fashion to the various smut collections. Others, however, showed striking differences and thus furnished a basis for differentiating the collections.

Ten varieties of oats have been useful in separating out the races of covered smut, and 17 varieties have served for the races of loose smut. It must be emphasized that definite strains of these varieties have been used in these experiments. Other strains of the same varieties or species may give different results. In the tables, the seed numbers which designate them are given, along with the accession numbers of the division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

In an earlier publication (Reed, 1929), numbers were given to 11 specialized races of *Ustilago avenae* and 5 of *U. levis.* In order to avoid possible confusion, the original race numbers have been retained, although it might be more convenient to renumber the races on the basis of their apparent relationship.

Keys for differentiating the races are given. These are based upon the reaction of the oat varieties, whether they are susceptible or resistant. Suscep-

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