ROOT DEVELOPMENT OF WHEAT, OATS, AND BARLEY UNDER CONDITIONS OF SOIL MOISTURE STRESS

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INTRODUCTION

Drought is an important factor in limiting cereal production in the United States and indeed in many other parts of the world. A large proportion of the cereal acreage in this country is grown in the more arid regions, where cereals are better adapted than most other crops, but where drought frequently occurs. In Jordan more than four-fifths of the cereals are produced in regions where drought occurrence is a common phenomenon. Periods of drought at some time during the growing season are also common in the more humid areas.

The problem of testing for drought resistance is one of great importance, however, it is hampered in the field by the great fluctuations that occur from year to year and from location to location in drought incidence even in the arid regions. Thus the development of a satisfactory laboratory test would be of great aid in selecting for drought tolerance.

Many phases of drought tolerance have been investigated in an effort to establish a valid test for selection for drought resistance. The importance of the root system for the maintenance of water balance in the plant and as a characteristic of drought hardy varieties was observed by Weaver (83), Khanna and Raheja (35) and emphasized by Misra (49).

The ability of roots to penetrate into soils that have a moisture level below the permanent wilting percentage is a very controversial subject (31). Such an ability, it seems, is a hereditary characteristic depending on the plant species.

Species and varietal differences in respect to drought hardiness as reflected in laboratory experiments have been reported by several workers: Misra (49), Hunter and Laude (32), Pavlychenko (54), Bayles (3), Powell and Pfeifer (57), and others.

Root study, according to Pavlychenko (54), provides a key to a proper interpretation of the above-ground plant development, as the extent of the top growth, except for diseases and insects, is a direct result of the factors operating underneath the surface.

As wheat, oats, and barley are of great economic importance, and since the testing for drought hardiness is a major part of any plant breeding program in arid regions, the present study was conducted in an effort to determine the presence of any significant species or varietal differences in the behavior and early development of their root systems under conditions of soil moisture stress. Such differences, if established, may be used as a possible index for determining relative drought tolerance.

REVIEW OF LITERATURE

General

The importance of the root growth of plants has long been recognized as having an important bearing on agriculture. For the last two centuries strenuous efforts have been made to get a clear understanding of the underground parts of the plant. Harris (26) and Pavlychenko (54) presented brief reviews of the earlier work on the root systems of plants. Of the early workers mentioned were Hales (1727) who perceived the idea that the quantitative extent of root systems has a profound and direct bearing upon the productive potentialities of plants. Sachs (1865) showed that the more concentrated the nutrient solution the shorter the roots. Nobbe (1862, 1886) showed that roots branched more freely in soils which contain abundant food materials than in those which are poor in them. Volkens (1887) described the great root growth of plants in arid regions. In the Egyptian desert he observed that there were roots 20 times as long as the parts above ground. Fruwirth and Kraus (1895) presented some valuable data regarding the growth of roots especially at different periods in the life of the plants. Müller-Turgau (1897) did considerable work on the effect of nitrogen and of mixed salts on the growth of roots using potted plants. He observed that concentrated solutions of mixed salts retarded root growth, and that the best growth was in weak solutions. Overfertilization checked the growth of new roots.

Tucker and Von Seelhorst (1898) using soil containing three different moisture levels found that there were relatively more roots with low than with high soil moisture. They also found more roots in unfertilized than in fertilized soil. On the other hand, from tests with rye, spring and winter wheat, barley, peas, beans, and field beets, Von Seelhorst (1902) arrived at a contradictory conclusion. From a set of rather elaborate tests which were carried out with a uniform soil so arranged that he could determine the number of roots in each 25 cm. section to a depth of 150 cm., he concluded that plants when liberally fertilized not only have a longer root system, but those roots descended deeper into the soil and are thus able to better withstand drought. McCool (1913), at Cornell, and many others have demonstrated that various salts in solution affect the ratio of tops to roots (26).

Of the other early workers in the United States, Hays (27) in Minnesota, worked on the distribution of corn roots, King (54) in Wisconsin worked on the distribution of roots of most common field crops. Ten Eyck (73) and then Shepperd (67) made similar studies in North Dakota and Kansas.

Many of the early workers dealt with plants in the open, although some used potted plants or even water cultures.

It was not until the work of Cannon (14) who studied plants of the region about Tucson, Arizona, that the nature of the subterranean parts of plants became known. He showed that the roots of desert plants are not always of great length and deep penetration, but in fact that they may be in some cases very superficial.

Markle (45) investigated the root systems of plants in the region of Albuquerque in the valley of the Rio Grande. He concluded that the root systems penetrate rather deeply, but often have prominent laterals near the surface of the soil. The cacti and a few of the shrubs have a very superficial root system. Storage roots he found uncommon, but were found to be more characteristic of more moist situations. He considers variation in soil permeability and its moisture content as two factors that affect root production.

Weaver (80-87) has presented valuable contributions on investigations of the root habits of plants. He first investigated the roots of prairie species of southeastern Washington, then he covered the great plains, the sandhill region of Colorado up to the Rocky Mountains. He extended his work to study the root systems of grass associations of Kansas, Colorado, South Dakota, and Nebraska. As a result of over 80 examinations of the root systems of crop plants, under widely varying soil types and conditions of growth, he correlated the root development of cereals and some other crop plants with the different types of the natural vegetation. In his book "Root Development of Field Crops" (83) he presented a comprehensive account of the root development of crops in the United States as known up to 1926.

The quantitative studies carried out by Dittmer (21) on the root hairs of winter rye; and by Pavlychenko (54) on the roots of cereals deserve attention.

Methods Used in Root Studies

The earlier methods used were tedious, time consuming, and expensive. They mostly consisted of digging a trench to a depth of about five feet and of convenient width by the side of the plant to be examined. This afforded an open face into which one might dig with a hand pick or a sharp knife (81, 89). Various improvements on this method were later reported by Stoeckeler and Kluender (72) who used a light portable water pump to effect working of the soil surrounding the roots in the trenches. Tharp et al (74) reported on the use of a fine jet of water for studying root systems of wild plants in undisturbed habitats. Weaver and Voigt (85) developed a method whereby a monolith of soil was taken from the field back to the laboratory, and the roots then worked free of the soil by means of a jet of water.

The use of radioactive isotopes as tracers of absorbed nutrients offers advantages, since great sensitivity in detecting the absorbed elements is possible by electronic apparatus. Hall (25) studied the root systems of four species of crops: cotton, corn, peanuts, and tobacco by growing plants in soil containing "labeled" (P^{32}) phosphate fertilizer. The activity of the root system in different parts of the soil was calculated by measuring the specific activity (i.e. the ratio of radioactive phosphorus to total phosphorus) of the plant.

Burton et al (13) studied the root penetration, distribution and activity of grasses under drought conditions in deep sand using radioactive phosphorus (P^{32}). They transplanted "turves" of different grass species to areas in which radioactive phosphorus had been placed at varying depths down to 2.5 meters. The depth of the root penetration was assessed by measuring the radioactivity of the leaves when a survey meter was placed near them.

Boggie and Knight (8: I), and Hunter and Knight (8: II) developed a method of injecting radioactive phosphorus P^{32} at various levels into soil where the plants are to be studied. Maximum root depths and the amount of absorption in different soil horizons could thus be studied. Lipps et al (43) studied the root activity of alfalfa at various depths in the soil by placing P^{32} tagged fertilizer at depths varying from 0-8 feet in small 1 1/2 inch auger holes drilled around the plants to be examined.

Lithium chloride was used by Sayer and Morris (65) for studying the extent of corn root systems.

Potted plants in the greenhouse and other types of observation boxes have been used for detailed studies on individual root systems and for determining the effects of the various factors on the behavior of roots of different plants. Harris (26) used long glass tubes 7/8 inch diameter (rather too narrow) for sowing and observing the growth of roots of crop plants. He used the tubes inclined at an angle 30^{o} from the vertical, immersed in water at varying depths 6" to 60" from the soil surface. Kroemer quoted by Rogers (61) reported on studies on vine roots growing in concrete containers with a sloping glass wall, as observed from a darkened passage lit when required. Weaver (86) used large size containers for his "water absorbing power of crop plants at various soil levels" experiments. The cylinders were 1 to 5 feet diameter x 3 to 5 feet deep. They were buried in the ground during use. Ostermann was reported by Rogers (61) to have used a series of observation boxes for studies on potato root systems. Schindler was also reported to have used some large root observation boxes for observing apple roots in grass and clean culture (61). Dean (19) used small observation boxes of two sizes 16 3/4 x 10 1/2 x 2 3/4 inches and 24 x 36 x 13 1/4 inches, fitted with removable glass sides on both ends. Sideris (69) described a small box of 6 x 6 x 8 inches with four detachable sides for the study of absorption of individual roots by leading them through a cork into a corked flask containing a measured nutrient solution.

Breazeale and Crider (11) used glass cylinders 14 inches tall, 3 inches inside diameter, in which they grew plants for determining the behavior of seedlings, especially root functions and development when growing in soils of low moisture content. They placed the cylinders in holes in the ground slightly tilted. Bates (4) described a device for observation of root growth in the soil, consisting of lowering glass tubes closed at one end down holes and observing root development by a mirror torch device.

Rogers (63) recommended the use of "small" observation boxes for the comparison of certain treatments on the roots of small plants for one or two years. His boxes, however, were relatively large being 24" long, 17" deep, and 7" wide with vertical glass windows 24 1/2" x 15" reinforced with wire fitted to the two large sides. Each box held about 120 lbs. dry soil.

Linford (42) described a miniature root observation box for the use in studies on nematodes on roots under the microscope or binocular.

Partridge (53) used a galvanized iron container 10" x 10" in diameter and 4 feet deep with detachable side and bottom for grass root studies. Davis (18) used glass fronted wooden boxes for planting maize. Rate of growth and distribution of the roots were studied daily by observing the roots that could be seen through the glass. His boxes, however, were large and very heavy to handle.

Carter (15) described a method for observation of root development by growing plants in water vapor. Wadleigh et al (78) used wooden containers 1 foot square, 36" deep, to study root penetration in soil layers of varying salinity, of beans, corn, alfalfa and cotton plants.

Midway between observation boxes anf field observation trenches came the root observation chambers of Blaauw at Wageneningen (6). Kinman in California (36) used some simple glass walled observation trenches and observed the root growth of peach, apricot, and plum trees during two seasons. Rogers (61) used special modified observation trenches, with glass windows for continuous observation of fruit tree roots. Openheimer, as reported by Rogers (61), used root observation chambers at Jerusalem to study oak and pine roots. Pavlychenko (54) used a system by which the whole block of soil containing the entire plant is excavated, encased, and lifted up to the surface. Subsequent washing reveals the entire root system.

Root Habit and Drought Tolerance

Initial root habits are inherent characteristics. Modifications of root habits due to changes in external conditions are extremely variable in different species (75, 33). Rogers (61) stated that the varietal root habit is inborn in the plant and may persist so that the roots may be recognized under a wide range of environmental factors. As a result of his studies of the roots of apple trees, he concluded that although soil factors such as texture, nutrients, aeration, moisture and temperature control the root system to a large extent, yet within certain limits, varietal root habit seems to have the greatest effect on the type of growth, while soil factors affect the time of growth, i.e. growth activity during the life cycle of the plant.

Root studies as an index to drought resistance are rather limited in number. Walworth and Smith (79) reported that different varieties of a given cereal show characteristic tendencies in the production of the secondary seminal rootlets. They found that this tendency was greater in barley than in either wheat or oats.

Weaver et al (86) reported that the roots of wheat at the seedling stage spread more widely than oats, and were lighter in color, tougher, and although abundantly supplied with root hairs they did not occur in such density as in oats. The surface roots of wheat when compared with those of oats and barley are found to be both less numerous and extensive.

Weaver (82) and later Pavlychenko (54) emphasized the importance of depth and extent of root systems in enabling plants to develop normally under adverse moisture conditions. Ivanov, quoted by Cook (17), demonstrated this fact by his work on drought resistant plants in which he stated that the ability of a plant to resist drought is directly proportional to density and extent of root systems. In another publication, Weaver et al. (87) emphasized that resistance to drought in grass forbs is closely correlated with root extent. They were investigating the effects of the severe drought in the summer of 1934 on the native plants of the prairie region near Lincoln, Nebraska. They found that species with root systems penetrating 8 to 20 feet into the moist subsoil were little affected. Water content of tissues decreased but little with the progress of drought and increase in osmotic pressure was slight. When the root systems were shallow and less efficient, decrease in water content of tissues was pronounced, and increase in osmotic pressure was 8 to 38 atmospheres.

Worzella (89) studying root development of hardy and non-hardy winter wheat varieties found that in the non-hardy varieties studied, many of the seminal roots develop almost horizontally in the early stage of growth, then turn downward. In the hardy varieties most of the seminal roots run obliquely outward or straight downward.

Aamodt and Johnston (1) noticed that drought resistant spring wheat varieties possessed a more highly branched primary root system than susceptible varieties.

Pavlychenko (54) as a result of his extensive quantitative studies on the root systems of wheat and other crop plants, ascertained the existence of such varietal differences and presented figures for the numbers and total lengths of the root systems of wheat, wild oats, barley and rye. He found that wild oats produced the crown roots at a much earlier date and in much greater numbers than any of the other cereal crops, but has a small number of seminal roots in its earlier stages - a fact which indicates the possibility of it being smothered by other cereal crops in its early stages of development before its crown root system gets well established.

Collins (16) stated as a result of his studies on drought resistant strains of maize that seedlings of the hardy varieties lacked secondary root branches entirely and the root extended to greater depths than in the non-hardy varieties.

Hubbard (30) concluded that extensive root branching of the drought hardy varieties of spring wheat was responsible for their greater yields during drought periods. Noll (54) reported that during periods of extreme drought, shallow rooted wheat plants died, those of moderate depths suffered greatly and only deeply rooted plants functioned normally.

Ashley and Valerie (2) found that differences existed between oat varieties in the rate of growth after being subjected to drought and subsequent recovery. They suggested the use of this criterion as an appropriate measure of drought resistance.

Derick and Hamilton (20) emphasized the wide differences in the total mass of root growth as well as in the number and coarseness of anchorage roots in oat varieties. Platt (56) reported on the existence of varietal differences in the response of wheat varieties to artificial drought.

Cook (17) as a result of his investigation with *Bromus inermis* found that the resistant strains were consistently high in numbers of both "large" and "small" roots, and in most cases possessed a significantly greater average root depth than less resistant strains during the entire season. He concluded that total axial root length is one of the best single measurements for evaluating root systems of Bromus inermis, and that resistant strains possessed greater root weights in proportion to top weights than non-resistant.

Misra (50) maintains that root development is an important character associated with drought hardiness of crop plants. He concludes that the capacity of any variety or strain to develop a root system rapidly in the early stages of growth is an important feature of drought resistant plants. He found that the corn strains which possess better root systems have shown greater resistance to drought.

Availability of Soil Moisture for Plant Growth

Of the environmental conditions which greatly affect root development, soil moisture seems of most importance, especially where rainfall is scanty and where adequate supplies of irrigation water are lacking.

The supply of available moisture to plants in a soil is the total quantity than can be extracted from the profile in the plant growth and maturity process (33). Breazeale (10) considers the available moisture in a soil as that water which is held with a force of less than the suction force of the plant or a force of less than five atmospheres. Jamison (33) lists the plant, climatic and soil factors that affect the available moisture supply as being: a) Plant conditions including nutrients present, stage of growth, rooting habit, plant resistance to drought; b) Air temperature, air humidity including the effects of fog and wind; c) Moisture tension relations, soil solution, osmotic pressure effects, kind of ions present in the soil solution, soil moisture conductivity, soil depth, soil stratification including the effects of hardpan and external layering and soil temperature and temperature gradients.

The subject of soil moisture-plant relationship has been discussed thoroughly by Maximov (46), Kramer (39), Kelley (34), Richards and Wadleigh (60), Black (7), and Russell (64).

Early in the twentieth century Briggs and Shantz (12) showed that the lowest limit of moisture for uninterrupted growth of plants is the wilting coefficient of the soil. Soil moisture above this limit is available both for metabolic and transpiratory processes. At or below wilting coefficient, water in the soil is not readily available for transpiration purposes and plants enter their quiescent state of wilting when slow rate of water absorption continues to some extent until complete desiccation occurs. During the drying stage the plants are simply acting as the medium for the transfer of water from soil to air.

The question of availability of water to plant growth between field capacity and permanent wilting point, i.e. whether it is equally available throughout this range, or plants respond favorably to high moisture conditions and adverse effects result as the water content decreases, is rather controversial.

Veihmeyer and Henrickson (76) reported on this controversy and reviewed the literature extensively. They concluded that the hyperbolic nature of the relationship between soil moisture percentage and moisture tension accounts for the frequent findings that for all practical purposes plants may not show changes in growth responses while reducing the moisture percentage of soil from field capacity to nearly the wilting percentage.

Schneider and Childers (68) reported an increase in apparent photosynthesis with a slight decrease in soil moisture below field capacity.

Wadleigh and Gauch (78) concluded from a study on cotton plants that leaf elongation ceased at a moisture stress close to 15 atm. Richards and Wadleigh (60) stated that the available soil water for plant growth decreases progressively as soil moisture stress increases.

Jamison (33) stated that moisture availability and plant growth decrease progressively as the wilting range is approached. He believed that not all the "available" moisture supply is equally available to the plant until it is exhausted.

Gingrich and Russell (22, 23) concluded that in the absence of other limiting factors, radicle elongation and the increase in fresh weight, dry weight, and hydration of excised corn seedlings decreased with increasing soil moisture tension in the range of 1/3 atm. through 12 atm.

Kramer (40) considers the most immediate of several effects produced by moisture stress in decreasing the absorption capacity of the root system as being the increased resistance to water movement resulting in dehydration of cell membranes.

Slatyer (70) mentions that the first evidence of decreased growth occurs at quite low stress levels. He stresses the importance of the permanent wilting percentage in the study of the plant and soil water relations. He presented a comprehensive review of the work done in that field and concluded that the permanent wilting percentage is fundamentally a value determined not by any soil characteristics, but by the osmotic characteristics of the plant. He reported that most evidence on the decrease in growth and dry matter production was found in the treatments which allowed a significant depletion of soil water below field capacity. He also mentioned instances of reduction in growth and yield at soil moisture tensions as low as 0.7 atm. He believes that the reductions in growth are caused primarily by decreasing hydration in the plants.

Bennett and Doss (5) studying the effect of soil moisture level on root distribution of cool season forage species reported that the amount of roots and rooting depths varied with the species and soil moisture.

Root Habit and Penetration in Soil at Various Moisture Levels

(A) Above the Wilting Percentage

As early as 1875 Muller-Turgau (37) concluded that relatively dry soil conditions induced plants to develop a more extensive root system than did moist soil conditions.

Harris (26) observed that the longest and heaviest root of corn seedlings grown in long glass tubes under different moisture levels correlated with low rather than with high soil moisture, and that the moisture during the early stages of growth had the greatest influence on root development.

Earlier (1911), Cannon (14) stated that the depth to which the roots of annuals penetrate the ground was directly controlled by the depth of the penetration of the rains. Thus it appears that root persistency is directly dependent on the length of time the water remains in the soil. He further stressed that annuals with the deepest root systems were the longest survivors after the wet season had passed. The findings of Weaver (80) that great root depths correlated with deep soil moisture bear out Cannon's findings. In a publication in 1925 (82), Weaver reported that under 26 to 32 inches of precipitation, the tops of winter wheat were tall and roots were deep with relatively small lateral spread. From 16 to 19 inches precipitation, the tops were short and roots were shallow but very widely spreading and much profusely branched. Root habits under an intermediate precipitation of 21 to 24 inches fell between these two extremes, but were correlated with a medium development of shoot. (See also Ref. 83).

Weaver also found that in corn grown in soils with moisture contents of 9% to 19%, the absorbing area (excluding root hairs) was 2.2 and 1.2 times as great as the area of tops in the former and the latter soils, respectively. The total length of the main roots and diameter in the two cases were the same. In the drier soil 75% of the root area was furnished by the primary laterals and 14% by the branches from those. In the wet soils the primary branches furnished only 38% of the root area and 51% was furnished by an excellent development of secondary and tertiary branches. The main roots in both cases were not more than 11% of the total abosrbing area.

Weaver and Himmel (84) investigating root development in hydrophytes, reported that root depth increased with decreasing water content until the soil became too dry for root growth. This is in agreement with the earlier findings of Harris (26) that the longest and heaviest roots of corn seedlings grown in damp and in dry coarse quartz in glass tumblers for 14 days, were produced in the driest sand. Their weight was nearly 3 times more than the tops, while the weight of the roots in the wettest sand was only slightly more than the tops. Poor aeration in the moist soil may account for such poor development.

Worzella (89) found that in a warm, dry season, the roots of winter wheat grew more rapidly and penetrated to greater depths than in a cooler and wetter season. A depth of 70 inches was reported for the roots of some mature plants.

Breazeale and Crider (11) reported that the tendency toward branching was much more pronounced in the moist than in the dry soil from a split-root experiment with orange plants with the two roots growing, one in 5% moisture, and the other in 10%. The weight of the roots in the moist soil was much more than that in the dry soil.

Miller (48) presented evidence on the increase in weight of roots of corn, wheat, and barley in the soil with decreased water; i.e. that the root development varies inversely as the soil water content. Rogers (62) studying the roots of apple trees reported that moisture appears to act as a limiting factor to root growth well before the wilting range is reached. The degree of dryness at which root growth "check" occurred usually corresponded to a soil moisture tension of 30-40 cm. of mercury, or sometimes even lower.

Davis (18) reported that roots of established maize plants absorbed water from the soil more rapidly near the plant than at a distance of 3 or 4 feet. Roots of growing plants, he observed, extracted water below the wilting percentage in soil near the plant even though similar numbers of roots were present in moisture above the wilting percentage four feet away. The water four feet away was eventually absorbed after the soil near the plant was dried below the wilting percentage. He observed also that growth of the young plants was slowed by decreasing moisture and was stopped when the soil moisture percentage was still above the wilting percentage.

Khanna and Raheja (35) observed that plants differed but slightly in their ability to deplete the moisture content of any given soil.

Williams and Shapter (88) reported on significant yield reductions in barley and rye as a result of low water treatment. The severity of the effects on various plant parts was conditioned by the stage of development of those parts. An increase in the ratio of roots to shoots has been regarded as a typical response of plants to low water treatment.

Kmoch et al. (37) investigating the effect of soil moisture on the root development of winter wheat by wetting the soil to depths 0, 2, 4, 6 feet before seeding, reported that: In November, roots attained a depth greater than three feet in the 4 foot and 6 foot treatments and 2 1/2 feet for the 2 and 0 foot treatments with little top growth in all. Roots under the less favorable conditions were finer, and had more and longer branches. A dense network of roots developed in the soil which had received no supplemental moisture even though soil moisture tension was above 15 atm. at depths greater than 12 inches. April samples showed that living roots were confined to the regions of moist soil.

Total weights were highest when nitrogen had been applied and the depth of penetration was greatest for the treatment wetted to 6 feet. At harvest, roots to a depth of 13 feet were found where moisture conditions were favorable.

Bennett and Doss (5) reported that effective rooting depth decreased as soil moisture level increased. They found that over 70% of the total weight of roots of all species of the cool season grasses used in the test occurred in the surface 12 inches of soil (except tall Fescue).

(B) Root Penetration in Soils Below the Wilting Percentage

A wide difference of opinion exists as to the ability of the plant roots to extend into soil having moisture content below the permanent wilting percentage.

Shantz (66) believed that the roots of some drought resistant plants are able "to push" their roots into dry soil, but that ordinary crop plants lack that ability.

Magistadt and Breazeale (44) studying the soil moisture and root relationships noted that at the wilting percentage there was equilibrium between the plant and the soil with respect to moisture. To a certain extent, they surmised that the plant is probably able to maintain this equilibrium by exuding water from its roots whenever the soil moisture is reduced below the wilting percentage. They noticed that many desert plants have their roots coated with a thin layer or sheath of soil which,they believed,is a mechanical result of the exudation of water and probably some connecting material. This coating, they stated, helps to maintain the moisture content of the soil sheath at the wilting percentage of the soil when the latter is subject to drought, thus preventing desiccation of the root and turgor can be maintained.

Breazeale (10) suggested that a plant can absorb water from a moist soil or subsoil, transport this water, and build up the moisture content of a dry soil. Experiments with wheat and barley indicated that the roots of these plants could absorb water at lower depths and transmit it to other roots that were in drier soil at about the wilting percentage. He assumed that roots under such conditions could penetrate dry soil layers with no available moisture.

Hendrickson and Veihmeyer (28) concluded that - by using wax seals to separate the moist soil from the dry soil in the same container - the roots of sunflowers will not grow into soil which contains less moisture than is present at the permanent wilting point. In cases where roots penetrated the wax seal, they did not grow more than a few millimeters into the dry soil.

Breazeale and Crider (11) completed an extensive investigation on this subject and concluded that roots of certain plants were able to penetrated soils that were below the wilting percentage. A certain amount of dependence of one plant upon another may exist in nature in relation to their moisture supply. A deep-rooted plant may absorb moisture from the subsoil, transport this and exude it into the surface soil where a shallow rooted plant may absorb it, and thus tide over periods of stress.

The roots of Palo Verde (Cercidium torreyana) plants were found to elongate 3 cms. or more daily at 20°C. Rate of elongation was reduced as the available moisture was reduced to near minimum, and apparently stopped when the supply of water to all parts of the root system was exhausted. The roots first grew rapidly through the soil layers of 24.0% and 19.2% moisture and well into 14.0% layer. After 22 days the supply of available moisture was apparently exhausted in the top layer and all root elongation stopped. They found that the top layer lost moisture from 24.0% to 19.4%. The second gained slightly from 19.28% to 19.4%. The third from 14.0% to 16.3%. No penetration occurred in the lowest layer of 5.2% which was found to have increased to 9.1%. (They did not explain why.)

Similar results were obtained with catclaw (*Acacia gregii*) which they found its roots can grow into soil containing from 60 to 70% of the moisture it should hold at the wilting percentage.

They also proved that a tomato plant can absorb water from a moist soil, transport it to a dry soil and build the moisture content of the latter up to the wilting percentage.

Metzger (47) noted that alfalfa roots under dry conditions did not penetrate to as great a depth as when under conditions above the wilting percentage. Hunter and Kelley (31) studying the elongation of corn roots into dry soil obtained evidence of root penetration into the dry soil for an inch or so. They noted a slight increase in the moisture content of the dry soil, which they attributed to the persence of the roots. However, values as high as the wilting percentage were not obtained.

Muller (51) studying the gauyule rubber plant, found that its roots did not penetrate into dry soils. He noticed that as the soil in the root zone dried out, growth ceased and the roots became suberized. Volk (77) agreed with Hunter and Kelley (31) and showed that the roots of corn plants can penetrate dry soil below the wilting percentage, and that the moisture content of the dry soil would increase. He believes that single roots cannot penetrate dry soil alone, but that masses growing together in a "common front" can. He thinks that the root growth takes place as a result of the cooperative build up of soil moisture by the "common front" of elongation of numerous roots.

Hagan (24) could not obtain evidence in support of Breazeale and Crider (11), and he observed that very little moisture is lost from living roots to the soil at the permanent wilting percentage. Kramer (39) does not believe that an increase in the moisture content of the dry soil to above the wilting percentage would result when roots are in contact with dry soils; although he thinks that some loss of water from the roots may occur. He states that most roots in dry soil cease to elongate and become suberized.

The Use of Laboratory Techniques For Studying Drought Tolerance of Crop Plants

Results from laboratory or greenhouse experiments to get information about plant behavior in the field must be considered with caution. However, inferences usually drawn from such experiments are relative and should be supplemented with field experiments if the results are to be of any useful application. Hunter et al. (32) obtained the same order of relative resistance with seedlings subjected to artificial drought in the laboratory as was noted for the plant's behavior in the field.

Heyne and Laude (29) found that the reaction of corn seedlings to artificial heat correlated well with the behavior of the same strains under field conditions, and they concluded that the testing of the sedlings for heat resistance can be relied upon with considerable assurance for distinguishing genetic differences in the drought tolerance of larger plants of different strains of maize.

Bayles (3) got varietal differences in the amount of injury of some winter wheat varieties subjected to artificial drought corresponding with their known field behavior under drought.

Platt (56) concluded that artificial drought tests may be useful in eliminating low yielding lines or plants from hybrid populations.

Veihmeyer and Hendrickson (76) summarized the whole picture by stating that while the results of growing plants in containers may indicate trends, they should not be taken as conclusive unless confirmed by field trials.

MATERIALS AND METHODS

Three consecutive experiments were carried out in the Botany greenhouse of the Oklahoma State University at Stillwater, Oklahoma, from early February until the end of May, 1962.

The cereals chosen for the study were hard red winter wheat (*Triticum aestivum* L.), winter oats (*Avena sativa* L.) and winter barley (*Hordeum vulgare* L.). These are known to possess varying degrees of tolerance to drought under field conditons.

From each of the above species two varieties were selected for their known contrasting reaction in the field under drought conditions [1] namely:

Wheat: *Cheyenne* (C.I. 8885), which rates among the best hard red winter wheats in its ability to withstand lack of water under Oklahoma conditions.

Ponca (C.I. 12128), rates "low" in its tolerance to lack of water under similar conditions.

Oats: *Wintok* (C.I. 3424), considered more drought tolerant than many oat varieties.

Arkwin Sel. (C.I. 7404), less tolerant to drought than Wintok.

Barley: *Ward* (C.I. 6007), considered drought tolerant under field conditions.

Rogers (C.I. 9174), possesses low tolerance to drought and ranks in a similar manner as Arkwin oats and Ponca wheat.

1/Based on oral information from Dr. A. M. Schlehuber, in charge of Small Grains Investigations, Agronomy Department, Oklahoma State University 7/14/1962.

The seed for all the experiments was obtained from the Small Grains personnel of the Agronomy Department at Oklahoma State University, Stillwater.

Wooden boxes specially designed for single plant root studies were used (Fig. 1). Each box measured 10 x 11 cm. across and 60 cm. in depth and were made of wood 3/4 inch thickness on three sides with a removable glass front fitted with 3 mm. glass which slides in grooves made on the two opposite sides. Protection against light was effected through a wooden door fitted on the inner surface with a piece of cardboard the same size as the glass, and fastened on the side by a latch which insured tight closure. Two 3/4 inch holes were opened on the back side of each box at a distance of about 15 cm. from either end. These holes served in taking soil samples for moisture determinations without disturbing the soil near and around the roots. The holes were kept tightly closed with cork when not in use.

The boxes were rather light and easy to handle. Each box contained about 14.5 pounds of soil. They were used tilted at an angle of 45^{o} degrees to allow the roots to grow against the glass front.

The soil used in the experiments was made up of two different mixtures. One mixture consisted of two parts per volume Norge loam soil, one part washed river sand and one part peat moss. This was used in all the experiments as the "top soil". The other mixture was made up of two parts per volume Norge loam soil, and one part sand, and was used as the "bottom soil". The pH of the top layer was 7.55, that of the bottom layer was 7.10.

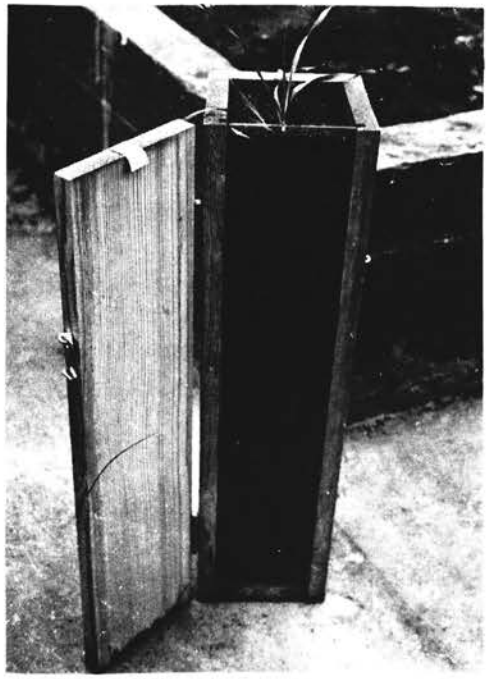

Figure 1. Glass-fronted wooden boxes used.

The depth of each soil layer varied with each experiment. Sowing was done by placing 3 seeds in the top layer of each box, next to the glass, and equally spaced to a depth of 1.5 to 2 cm. Water (25 cc.) was applied to the surface of the soil directly after sowing. As soon as the seeds germinated, two seedlings were pulled out, leaving one seedling - usually the central one - per box.

The temperature in the greenhouse was set at a maximum of 70°F. During the winter months it stayed fairly constant, but with the onset of spring, it rose up on sunny days, and maxima of 100°F were not uncommon. The average daily readings taken at about 5 P.M. were 72.6°F, 78.3°F, and 87.0°F for the duration of the first, second and third experiments, respectively.

No measurements of the relative humidity were made, but due to watering of the potted plants and other seed beds it is believed that the R.H. was never below 70%. It actually ran to a much higher percentage after placing wet mats on the west side late in April to help cool the house. The presence of two suction fans helped to maintain adequate distribution of heat and humidity in the greenhouse.

First Experiment. This consisted of 24 experimental units (boxes with a single plant each), arranged in a split-plot randomized block design. The species were the main plots within each of which the two varieties were randomized. Each replicate was placed on a bench, and all boxes were arranged in rows tilted at an angle of 45° from vertical and were facing south[2].

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[2]/Stillwater is on long. 97.12 W and lat. 36.6 N.

The boxes contained 25 cm. of "bottom soil" and 35 cm. of "top soil". The moisture content of the "top soil" was 11.1% while the "bottom soil" was air-dried to 1.6% moisture at the outset of the test.

Assuming no interaction between species and varieties, the varietal differences were measured within each species by analyzing the four replicates of every species as a randomized block design with two treatments in each block. The test for differences between species was carried out in accordance with the analysis of variance for split plot designs as outlined by Steel and Torrie, P. 236 (71).

Second Experiment. The same layout and the same varieties as for the first experiment were used. The depth of the "top soil", however, was reduced to only 15 cm. in order to study the ability of the roots to penetrate dry soil below the wilting percentage at the early stages of growth.

The bottom layer used was air-dried to 2.3% moisture content. Initially the top layer had a moisture content of 12.6%.

Third Experiment. This was aimed at comparing the root behavior of each of two species under four different levels of moisture stress. The two species were oats (Wintok) and barley (Rogers). The boxes were filled with "top soil" to a depth of 15 cm. which had 17.4% moisture. The "bottom soil" which was used to fill the remaining 45 cms. of each box had the following moisture content:

Treatment I: 4.3% equivalent to 10 atm. moisture tension.

Treatment II: 5.1% equivalent to 6.5 atm. moisture tension.

Treatment III: 8.1% equivalent to 1 atm. moisture tension.

Treatment IV: 10.5% equivalent to 0.45 atm. moisture tension.

Soil moisture tension was determined in the soil physics laboratory using a pressure membrane apparatus as described by Richards (58) for tensions above 1 atm. and by an adapted pressure cooker apparatus fitted with a porous ceramic plate as also described by Richards (59). Appendix (I) shows the relations of the moisture content and the soil moisture tension of the "top" and "bottom" soils used.

At the end of each experiment roots were removed from the boxes almost intact by first removing the glass cover and then gradually lifting the roots starting from the top, with any soil that might be attached to them, using a knife as an aid in lifting the soil in the vicinity of the roots. By careful and gentle hand tapping on the spread out root system, the soil could be shaken off easily without damaging the roots. (The soil at the time of root extraction was very dry in all experiments).

The measurements taken included daily growth records of roots and shoots, numbers of roots in the main root system as observed through glass and as found after roots were removed from the boxes, root lengths and dry weights of roots and tops. Photographs of the different treatment combinations were taken at the termination of each experiment. All data were subjected to statistical analysis.

In addition to the above experiments, an observation test on two drought resistant grasses[3] was carried out for the purpose of studying the ability of their roots to penetrate soil below the wilting percentage. The grasses used were Sand Love grass (Eragrostis trichodes Nash) and side oats grama (Bouteloua curtipendula Torr.). For this purpose wide-mouthed 3 inch glass jars, 8 inches tall were used. Each jar was filled to a depth of 10 cm. with "top soil", the rest was filled with air dry "bottom soil". A few seeds of each of the above grasses were sown in each of four jars. Water was applied in a very restricted quantity to the top layer only (25 cc. at sowing time). No more water was given until complete wilting occurred and the plants appeared to be close to death, when a similar quantity was again given on two occasions at 2 day intervals. No more water was added up to the termination of the test.

3/Provided through the courtesy of Mr. Robert Ahring, U.S.D.A. grass seed laboratory, Stillwater.

EXPERIMENTAL RESULTS

First Experiment

The duration of the experiment was six weeks, (February 16 to March 24, 1962). The weather was generally cool, and the greenhouse temperature was controlled to a maximum of about 70°F, which was maintained during the first four weeks. During the fifth week, however, the day temperature was up in the 80's. The mean temperature was 72°F.

There was no noticeable difference in the germination date between varieties. The roots started growth about four days before the first leaf emerged above the soil. There were obvious differences in the number and length of the primary roots at this early stage, as can be seen from Table I.

TABLE I

NUMBER AND LENGTH OF ROOTS
ONE DAY BEFORE EMERGENCE OF FIRST LEAF

(Averages of four plants)

	Wheat		Barley		Oats	
	Cheyenne	Ponca	Ward	Rogers	Wintok	Arkwin
Number of Roots	3.0	2.3	4.3	4.5	2.7	2.5
Total Length mm.	86.0	80.8	94.0	91.0	58.8	60.8
Length per Root mm.	28.7	35.1	22.1	20.2	21.4	24.3
Species average of total root length	83.4		92.5		59.8	
S.E. for total length (between species = 10.41 mm.)						
L.S.D. 5% = 25.47 mm.						
L.S.D. 1% = 38.58 mm.						

The differences in root length within each species were not significant.

Oats had the smallest root system at this stage. The barley, with the largest number of roots per seedling, had the widest lateral spread, whereas the roots in oats and wheat tended to grow directly downward.

The effect of soil moisture on the growth of both the roots and the tops was clearly demonstrated. As the moisture content of the soil decreased, the rate of growth decreased accordingly (Figs. 2-4).

It is interesting to note that the roots appear to be affected first while the tops show the effect of decreased development two to four days later. In nineteen out of twenty-three plants[4], the roots stopped growth before the tops (Table II). First plants to discontinue root growth were Ward barley followed by Cheyenne wheat, when the estimated moisture content was about 8.2% (Fig. 5). Shoot growth activity continued at this stage, although at a slower rate.

The maximum number of roots came to a stop when the moisture content of the soil dropped to an estimated 6.7%[5] on the 3rd of March, when all wheat plants, half the barley plants, and one quarter of the oat plants stopped all root gorwth. The tops, on the other hand, continued growth on a reduced scale in all wheat plants, three quarters of the barley plants and one quarter of the oat plants.

4/One wheat plant missing.

5/Calculated permanent wilting percentage in top soil = 6.4% moisture content (Appendix I).

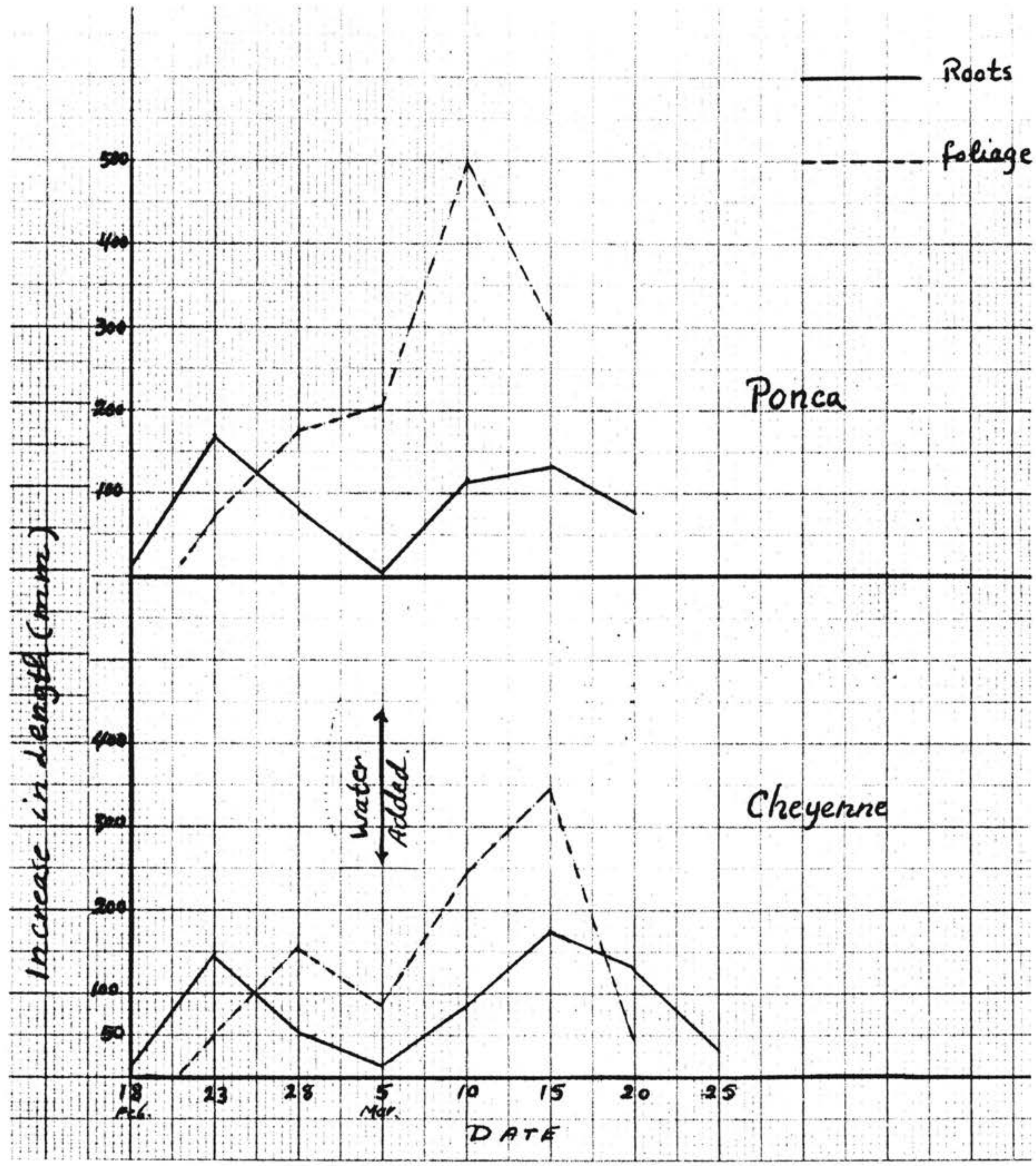


Figure 2. Increase in length per root and for total foliage in wheat.

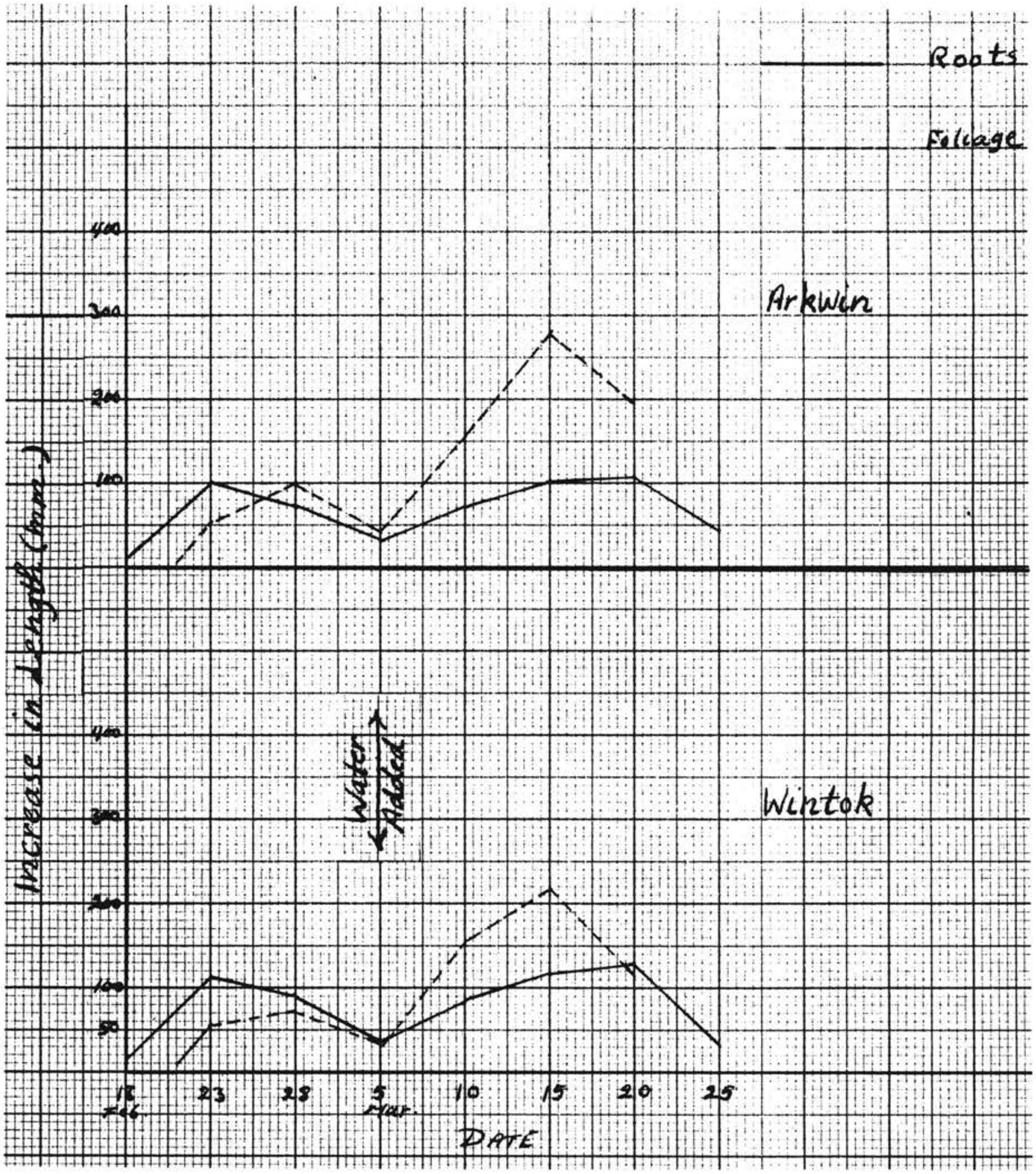


Figure 3. Increase in length per root and for total foliage in oats.

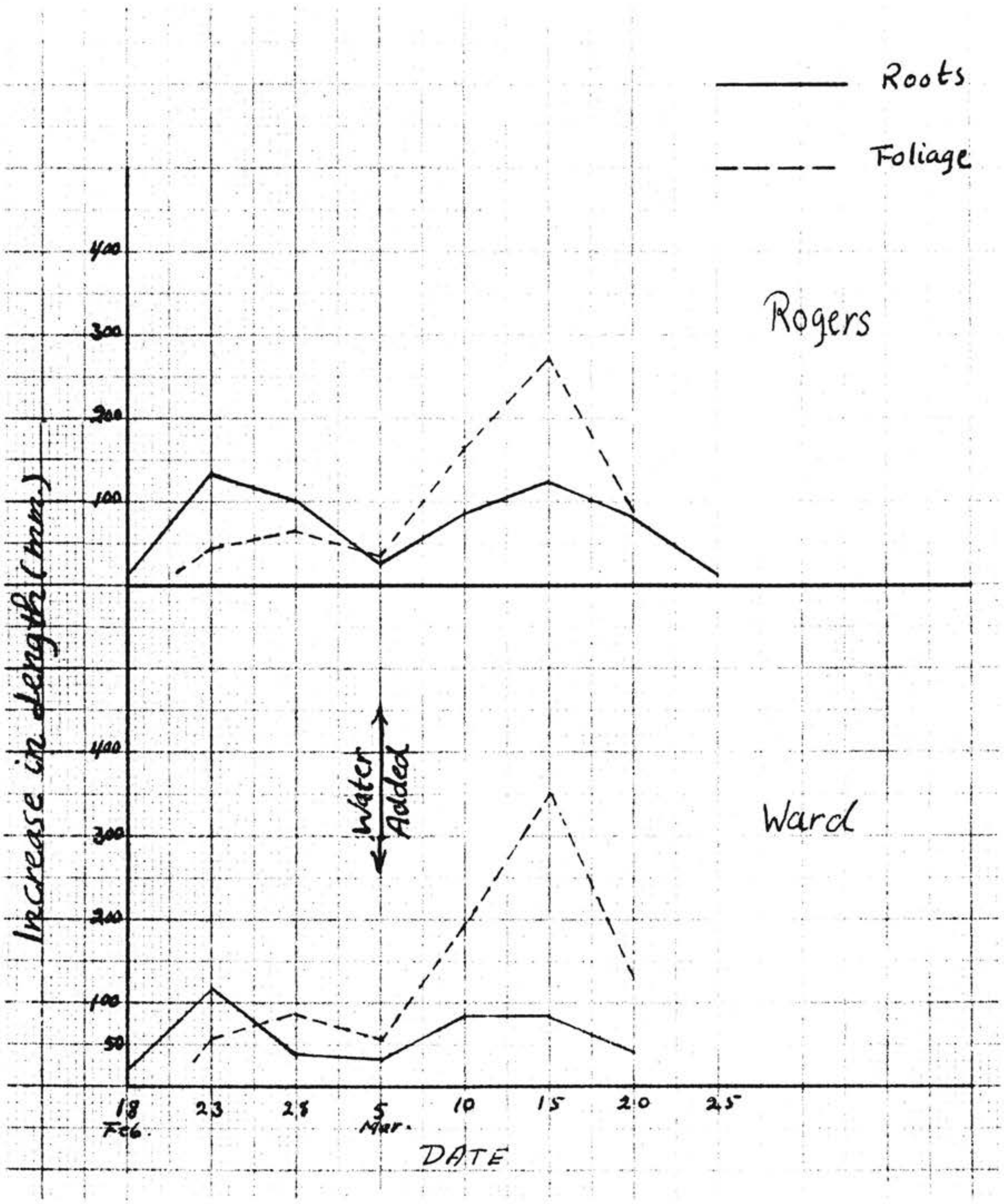


Figure 4. Increase in length per root and for total foliage in barley.

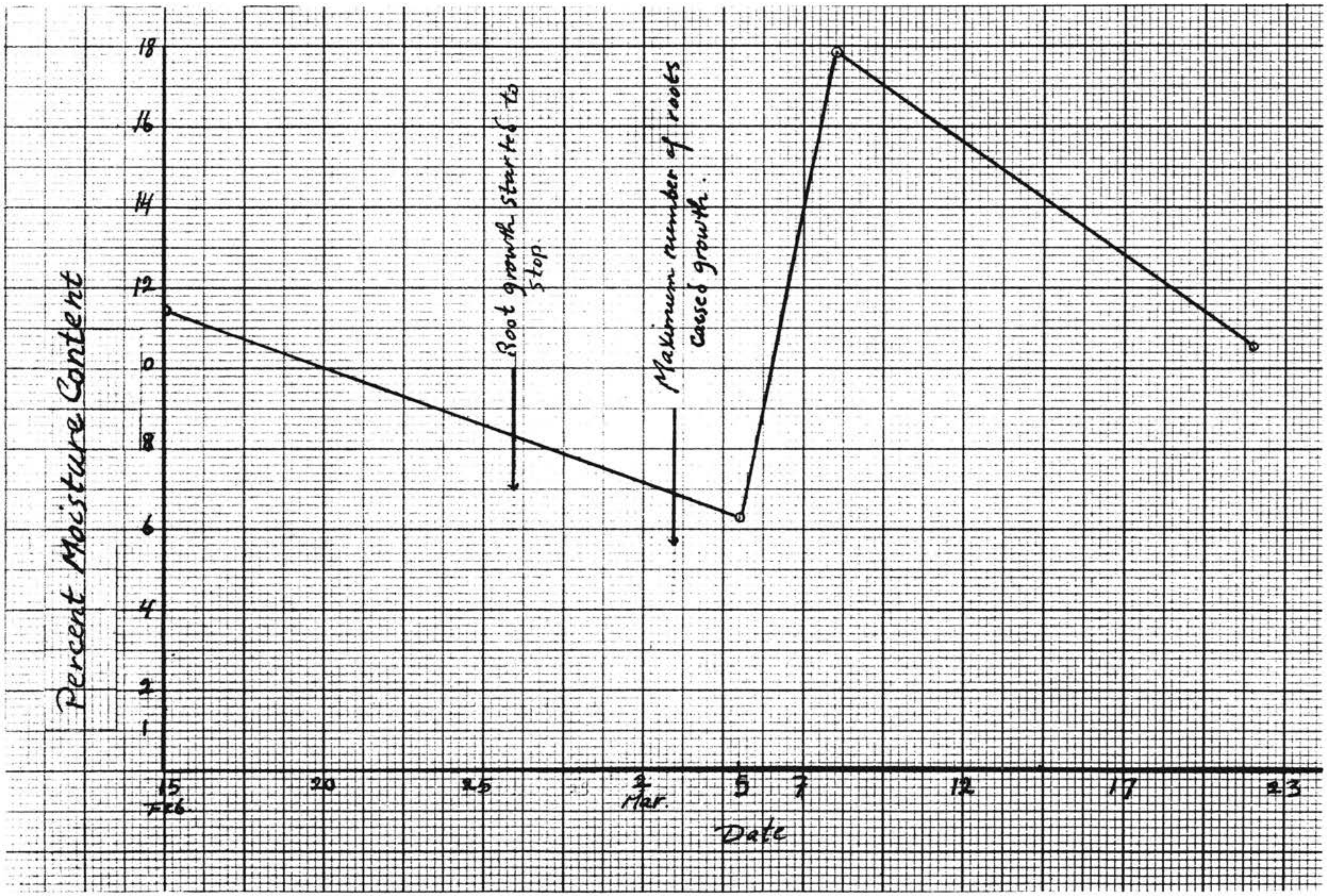


Figure 5. Moisture content of "top soil" in the first experiment.

TABLE II

DAILY COUNT OF NUMBER OF PLANTS WHOSE
SHOOTS OR ROOTS STOPPED GROWTH

Date	Roots Stopped Growth						Shoots Stopped Growth					
	A Plants *			B Plants**			A Plants			B Plants		
	Wh.	Bar.	Oat	Wh.	Bar.	Oat	Wh.	Bar.	Oat	Wh.	Bar.	Oat
Febr. 24	1	2										
25	1	2										
26	1	2										
27	1	2										
28	1	2			1						1	
March 1	2	2		1	2			1	1		1	
2	2	2		3	2			1	1		1	1
3	4	2	1	3	2	2		1	1		1	1
4	4	2	1	3	2	2		1	1		1	1
5***	4	2	3	3	2	3		1	1		1	
6	1	2	1	2	1	2						
7	1	2		1	1	1						
8	1			1								
9				1								

*"A" plants are Cheyenne wheat, Ward barley and Wintok oats.
**"B" plants are Ponca wheat, Rogers barley and Arkwin oats.
***All plants watered.

Resumption of activity after watering[6] the top soil was general. It was exhibited mainly in abundant leaf growth, and in the formation of new leaves. Root responded two or three days or more later, as in Ponca wheat.

Crown root development started after watering in almost all plants; and although seminal roots retained some activity, the main development shifted to the new roots, and many of the older roots appeared yellowish and very thin especially in oats and to a less extent in wheat.

Again, the root activity gradually decreased down as the soil moisture decreased (Figs. 2-4). There was a definite difference, however, in the time required for each species to discontinue growth, although no significant varietal differences within each species were detected (Table III).

TABLE III

NUMBER OF DAYS OF ROOT GROWTH AFTER WATERING

	Wheat		Barley		Oats	
Replicate	Cheyenne	Ponca	Ward	Rogers	Wintok	Arkwin
1	13	13	5	8	19	19
2	18	--	13	19	19	19
3	18	9	13	11	14	14
4	16	15	14	11	14	17
Variety Average	14.25	12.3	11.25	12.25	16.50	17.25
Species Average	13.29		11.75		16.87	
S.E.M. (For species) = 1.8 days L.S.D. 5% = 4.4 days 1% = 6.6 days						

6/Water applied to top layer only. (500 ml. per box).

The large variation in the individual plants probably accounts for the absence of significance within the species. A large number of experimental units may in such a case, be more adequate to detect such variation.

It is clear, however, that oats had the longest survival period.

The average daily growth of the roots, taken throughout the test until growth finally stopped, did not reveal any significant differences between the three species. A valid difference at the 10% level of significance, however, was detected between the two barley varieties, Ward and Rogers as seen in Table IV.

TABLE IV

AVERAGE DAILY ROOT GROWTH IN MM. OF ROOT/PLANT

	Wheat		Barley		Oats	
Replicate	Cheyenne	Ponca	Ward	Rogers	Wintok	Arkwin
1	20.2	22.1	15.9	22.2	15.6	16.8
2	18.6	----	12.3	17.2	16.8	17.3
3	21.6	21.3	12.0	20.3	19.9	16.5
4	19.8	19.5	20.5	21.4	23.2	13.9
Variety Average	20.1	20.9	15.2	20.3	18.9	16.1
Species Average	20.5		17.7		17.5	
	S.E.M. = 2.26 mm. L.S.D. at 10% = 4.39 mm.		Between the barley varieties			

Other data of interst including dry weights of tops, of roots, ratios of tops to roots....etc. are represented in Tables V and VI. The latter is prepared

With modifications after a similar study by Pavlychenko (54).

Figure 6 shows one replicate after the roots were extracted and washed. This and other pictures emphasize that no appreciable differences between species were shown.

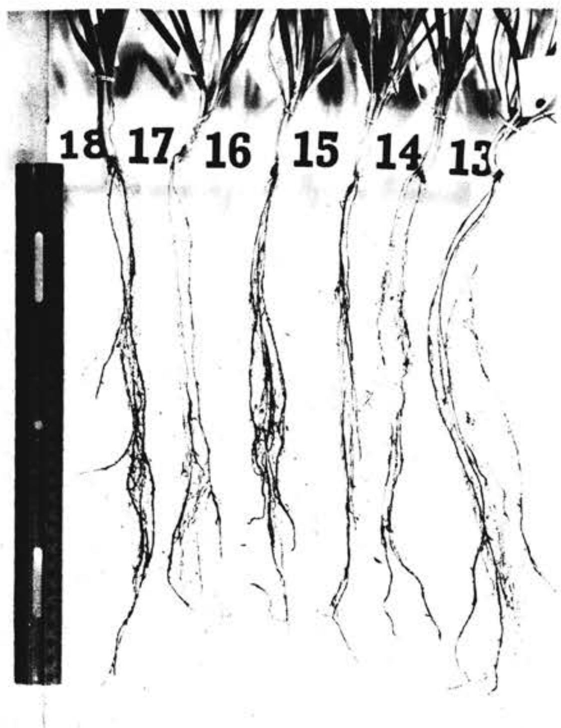


Figure 6. Roots of wheat, barley, and oats from first experiment. 13: Cheyenne wheat, 14: Ponca wheat, 15: Ward barley, 16: Rogers barley, 17: Wintok oats, 18: Arkwin oats.

TABLE V

SUMMARY OF DATA FROM FIRST EXPERIMENT
(Figures Based on Average of Four Plants)

Item Studied	Wheat		Barley		Oats		Remarks
	Cheyenne	Ponca	Ward	Rogers	Wintok	Arkwin	
1. No. of Roots							
a. Seminal	4.0	3.0	4.5	4.0	3.3	3.8	N.S.*
b. Crown	3.0	3.0	3.0	3.5	2.0	2.5	
2. Total Root length mm.							
a. Seminal	1127	779	883	694	843	858	Sign. for total between species. S.E.= 198
b. Crown	632	448	217	568	456	480	L.S.D. 5% = 486 mm.
3. Dry Wts (mgm)							
I. Roots							
a. Top 15 cms.	68.7	66.5	78.1	84.1	38.5	65.6	Bet. Spec. S.E.=8.75 mgm. L.S.D. 5% = 21.4 mgm.
b. Total Roots	119.6	98.0	123.9	128.4	70.3	107.3	N.S.
II. Tops total (mgm)	321.2	368.3	286.0	312.0	209.6	268.2	Sign. bet. sp. S.E.=22.0 LSD = 81.5 mgm 5% = 53.8
III. Top/Root	2.7	3.8	2.3	2.4	3.0	2.5	NS Bet sp. sig. within wheat

N.S. = Not Significant

TABLE VI

QUANTITATIVE STUDY OF MAIN ROOT SYSTEM OF WHEAT, BARLEY, AND OATS AS OBSERVED THROUGH THE GLASS FRONTS OF THE WOODEN BOXES AFTER 5, 15, 25, AND 35 DAYS OF GROWTH.

(Averages of Four Plants)

Characters Studied	Days After Emergence	Wheat				Barley				Oats			
		Cheyenne		Ponca		Ward		Rogers		Wintok		Arkwin	
The main root system		S*	C	S	C	S	C	S	C	S	C	S	C
A. Number	5	3.0	--	2.0	--	4.2	--	3.8	--	2.8	--	2.5	--
	15	3.0	--	2.3	--	4.0	--	4.0	--	2.8	--	3.0	--
	25	3.3	2.3	2.7	2.7	4.0	2.2	4.0	3.3	3.3	1.0	3.8	1.3
	35	4.0	3.0	3.0	3.0	4.5	3.0	4.0	3.5	3.3	2.0	3.8	2.5
B. Length less Branches mm.	5	299.8	---	269.7	---	207.2	---	297.5	---	182.0	---	161.8	---
	15	583.0	---	436.7	---	559.8	---	541.0	---	501.5	---	463.0	---
	25	960.0	360.0	667.0	241.0	756.0	104.0	657.0	282.0	838.0	123.0	698.0	82.0
	35	1127.0	632.0	779.0	448.0	883.0	217.0	494.0	568.0	843.0	456.0	858.0	480.0
C. Greatest Length mm.	5	152.0	---	165.3	---	137.5	---	149.5	---	116.2	---	99.8	---
	15	256.5	---	298.7	---	244.3	---	281.5	---	264.7	---	235.2	---
	25	339.8	217.0	298.7	152.0	323.5	80.0	206.0	146.0	320.5	40.0	304.0	57.5
	35	340.3	308.0	298.7	225.0	331.5	118.5	306.0	178.2	323.0	274.2	304.0	242.5

*S = Seminal; C = Crown roots.

Second Experiment

This experiment was carried out from the 28th of March to the 29th of April, 1962. The greenhouse temperature was higher than for the previous experiment. An average reading at 5 P.M. of 78.3°F was recorded. The moisture content of the top soil at the start of the experiment was 12.6% equivalent to slightly over 1/3 atm. tension; for the "bottom soil" it was 2.3% or well below the estimated wilting percentage[7] (3.8%).

The active growth period was short due mainly to the shallowness of the "top soil" with the more favorable conditions, coupled with more water loss from the surface soil due indirectly to higher atmospheric temperature.

Most root growth stopped soon after reaching the dry soil surface, yet in some plants, root growth continued for a few more days although at a much slower rate (Table VII).

TABLE VII

DAYS OF ROOT GROWTH BEFORE AND AFTER REACHING THE DRY "BOTTOM SOIL"

Repl.	Wheat				Barley				Oats			
	Cheyenne		Ponca		Ward		Rogers		Wintok		Arkwin	
	Bef	Aft	Bef	Aft	Bef	Aft	Bef	Aft	Bef	Aft	Bef	Aft
1	4	2	4	1	4	1	4	1	4	1	5	1
2	6	0	4	1	4	2	5	3	5	4	8	0
3	4	1	4	2	3	2	4	4	6	0	6	1
4	4	1	4	2	3	3	3	3	10	0	5	2
Av.	4.5	1.0	4.0	1.5	3.5	2.0	4.0	2.8	6.2	1.2	6.0	1.0

[7] The wilting percentage is considered to correspond to the moisture content of the soil at 15 atm. pressure (60). Apendix I.

Active root growth was recorded for the first three days in all varieties. The growth rate, however, was greatly reduced after the emergence of the first leaf. It practically stopped in nearly all plants 2 to 3 days after the shoot emergence, while the latter continued growth until it finally wilted (Table VIII). Growth rates, dry weights, length measurements and other relevant information are also presented in Table VIII.

Water was applied at the rate of 250 ml. per box to the top soil on March 18 after all plants showed "complete" wilting. Recovery was very slow and mainly in the shoots. Little root activity was recorded and only in two Barley plants (Rogers), one Wintok oats and two Arkwin oats plants. In general, barley was the last to wilt completely before the termination of the test on the 29th of April, when all the oat plants, one-half of the wheat plants and only three out of eight Barley plants showed complete wilting.

Folding of the leaves was observed mainly in Arkwin oats and Ward barley.

Third Experiment

The purpose of this experiment was to study the pattern of root development and penetration into soil at different moisture levels. The four moisture levels used were (at the start of the experiment): 10 atm. tension for treatment I, 6.5 atm. for treatment II, 1 atm. for treatment III, and 1/2 atm. for treatment IV.

TABLE VIII

DAYS OF ROOT AND SHOOT
GROWTH AND OTHER GROWTH DATA

(Second Experiment)

	Wheat			Barley			Oats		
	Cheyenne	Ponca	Aver.	Ward	Rogers	Aver.	Wintok	Arkwin	Aver.
Period of: Active Root Growth	3/31-4/5	3/31-4/5	6 days	3/31-4/5	3/31-4/5	6 days	3/31-4/5	3/31-4/5	6 days
Active Shoot Growth	4/5-4/18	4/5-4/22	16 days	4/4-4/21	4/4 4/14	15 days	4/4-4/17	4/4-4/20	15 days
Total Root Length up to emergence of 1st leaf: mm.	126	124	125	114	143	129	132	110	121
Total Root Length (actual)mm. *	325	414	369	575	476	526	431	467	449
Daily Growth Rate of Roots mm. ** ##	25.2	32.8	29.0	23.7	22.8	23.2	24.9	21.6	23.2
Total Dry Weight of Root mgm.	8.0	13.4	10.7	11.6	11.00	11.2	8.0	10.6	10.5
Daily Shoot Growth##	9.5	15.8	12.6	10.6	9.1	9.9	11.3	11.6	11.4
Dry Weight Ratio of Tops to Roots*	2.6	2.1	2.3	2.2	2.5	2.3	3.3	3.5	3.4

Table VIII (Continued)

	Wheat			Barley			Oats		
	Cheyenne	Ponca	Aver.	Ward	Rogers	Aver.	Wintok	Arkwin	Aver.
Ratio of Daily Rate of Growth Shoot/Root	0.42	0.50	0.46	0.46	0.54	0.50	0.48	0.55	0.55
Total Root Penetration In Bottom Soil mm. ≠	9	28	19	48	33	41	15	7	11
Maximum Root Penetration mm. **	7	15	11	25	22	23	4	8	6

** Significant differences at 5% level among species.
* Significant differences at 10% level among species.
≠≠ Significant differences at 5% level within wheat only.
≠ Significant differences at 10% level within wheat only.

The experiment was carried out between May 4 and June 10, 1962. During this period the relative humidity in the greenhouse was at a maximum due to the installation of wet mats on the west side to help cool the house. The average temperature recorded at 5 P.M. for this period was 87.0°F.

Here again root growth was very rapid after germination. No differentiation in the rate of growth between the various treatments was observed until the roots reached the bottom soil which was at different moisture levels.

The daily growth rate of the roots at this stage was much higher in the barley than in the oats. The number and total length of the primary roots was also higher in the barley seedlings than in the oat seedlings (Table IX).

TABLE IX

NUMBER AND AVERAGE DAILY GROWTH OF ROOTS PRIOR TO LEAF EMERGENCE
(Average of three plants)

Variety	Wintok Oats					Rogers Barley				
Treatment	I	II	III	IV	Av.	I	II	III	IV	Av.
Number of Roots Per Plant **	2.3	2.3	3.0	3.6	2.8	5.2	4.0	4.0	5.4	4.6
Daily Growth mm. (1)**	49	46	57	59	53	116	130	128	128	125
Total length of Primary Roots mm. (2)**	1110	1240	1300	1150	1200	2330	2540	2570	2930	2592

**Highly significant differences between the variety means at all moisture levels

(1) S.E.M. = 15.7
L.S.D. 1% = 155.7 mm/day
5% = 67.5 mm/day

(2) S.E.M. = 19.1
L.S.D. 1% = 180.5 mm.
5% = 82.1 mm.

Both oats and barley roots reached the "bottom soil" at almost the same time - on the 6th or the 7th day after germination. The barley, however, exhibited a wider lateral spread, while the oats roots pursued a more direct downward growth.

Root penetration into the "bottom soil" was found to be directly proportional to the soil moisture level (Fig. 7). This was exhibited by the two varieties used and to the same extent (Table X).

TABLE X

TOTAL ROOT PENETRATION (EXCLUDING LATERALS) IN "BOTTOM SOIL" AT VARIOUS LEVELS OF MOISTURE STRESS*

Moisture Level	Wintok Oats				Rogers Barley			
	I	II	III	IV	I	II	III	IV
Total Penetration mm./ Plant								
Rep. 1	68	230	696	869	118	249	656	824
Rep. 2	140	411	737	1011	175	397	702	1046
Rep. 3	279	189	784	518	164	202	515	906
Treatment Average mm.	162	277	739	799	152	283	626	925
Species average mm.	494.3				496.1			

Differences in root penetration at the various moisture levels are highly significant.

S.E.M. = 66.8

L.S.D. 1% = 211.7 mm.

L.S.D. 5% = 148.8 mm.

*Figures represent single plant readings in every replicate.

The active growth of the roots in the bottom layer was also proportional to the soil moisture content, the higher the moisture content, the longer the activity of the roots was preserved and a higher rate of daily growth was

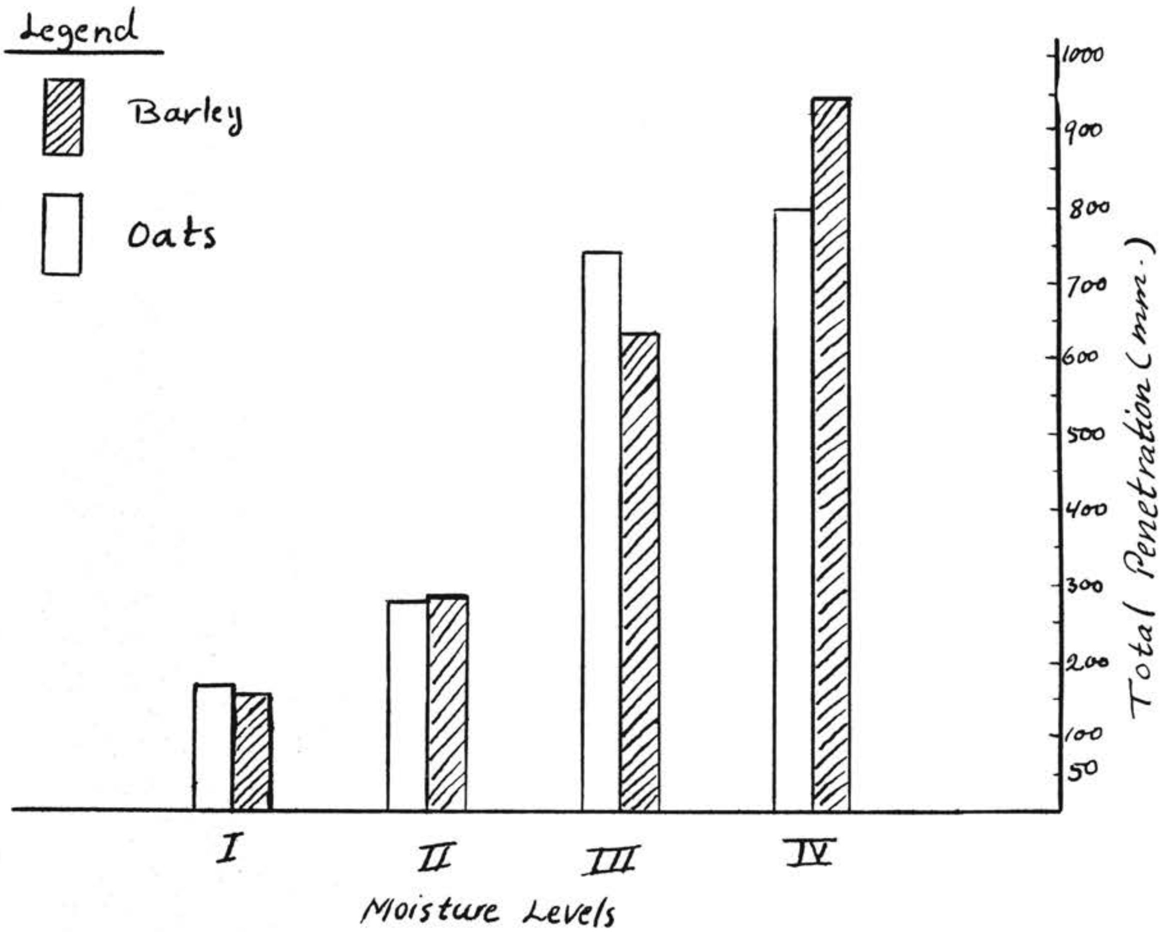


Figure 7. Root penetration into soil at different moisture levels.

maintained (Table XI).

Lateral root development was most pronounced in the treatments with low moisture content. In both treatments I and II for both barley and oats, most laterals started at about the 6th to the 8th centimeter below the root origin and increased in length and number in the region about 3 to 5 centimeters above and below the line separating the two soil types. In treatments III and IV, where there was more available moisture, few laterals developed in the top layer, and those which developed were not long. More laterals developed after the 10th to 12th centimeter, then less laterals for a few more centimeters, and again another group developed at about 5 to 15 centimeters above the root end. This was shown clearly in the higher dry weights obtained for the roots of both oats and barley in the treatments with the highest moisture stress. Table XII presents some measurements of interest which help to clarify the above point. Reference is also made to Figure 8 which shows the whole root system after excavation from the boxes.

The pattern above the soil surface, however, did not show any specific trend. The individual pattern variation was rather high in general. The plants which grew under the least moisture tension, however, tended to develop more leaves - especially in the oat variety - than those growing under higher moisture stress. Some dry weight differences were also recorded (Table XIII).

After more than three quarters of the plants of each variety were completely wilted, a small quantity of water (150 ml.) was applied to the top soil. Barley was watered on the 5th of June, whereas oats was watered three days

TABLE XI

DAYS OF ACTIVE ROOT GROWTH AND DAILY ELONGATION
OF MAIN ROOTS IN "BOTTOM SOIL" AT
VARIOUS MOISTURE LEVELS

(Averages of three plants)

	Wintok Oats					Rogers Barley				
Moisture Levels	I	II	III	IV	Av.	I	II	III	IV	Av.
Days of Active Root Growth (1)**	5.6	9.0	17.0	16.7	21.1	7.0	10.6	15.3	16.7	12.4
Total Daily Elongation mm. (2)**	24.5	29.9	43.9	44.9	35.8	25.8	25.9	43.8	47.6	35.8
Ratio of Root Length in Bottom Layer to Total Root Length (3) **	0.27	0.40	0.64	0.65	0.49	0.29	0.38	0.45	0.58	0.43

**Differences between "moisture level" means are highly significant.

	(1)	(2)	(3)
S.E.M. :	2.86 days :	5.47 mm/day :	0.05
L.S.D. 1% :	8.7 days :	17.3 mm/day :	0.15
L.S.D. 5% :	6.2 days :	12.2 mm/day :	0.11

TABLE XII

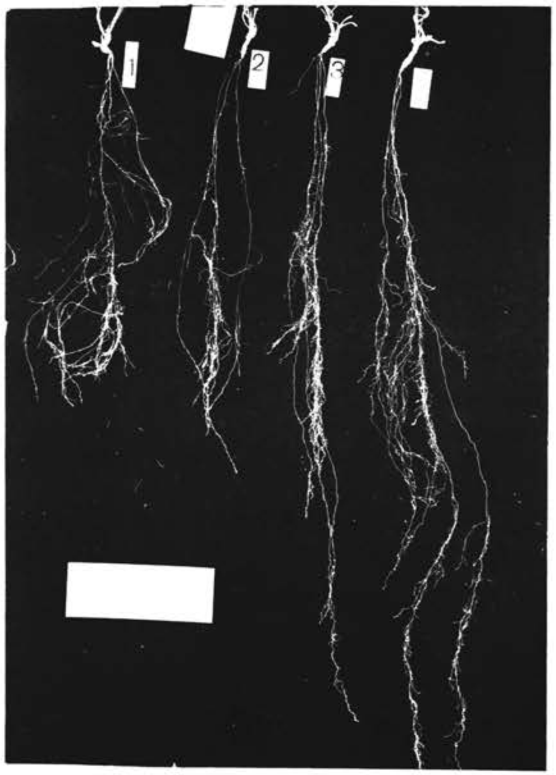
SOME ROOT MEASUREMENTS AT DIFFERENT MOISTURE LEVELS BASED ON THE AVERAGES OF THREE PLANTS

	Wintok Oats					Rogers Barley				
Moisture levels	I	II	III	IV	Av.	I	II	III	IV	Av.
Total Root Length mm. (Laterals excluded) (1)	566	677	1165	1159	892	1037	801	1399	1612	1212
Dry Wt. of Top 15 cm. of the Root System mgm. (2)	47.3	22.0	28.7	32.0	32.5	62.7	45.2	51.3	42.3	50.4
Dry Wt. of Remainder of Root System mgm. (3)	80.7	45.8	59.5	108.2	73.5	53.2	37.8	70.7	98.8	68.9

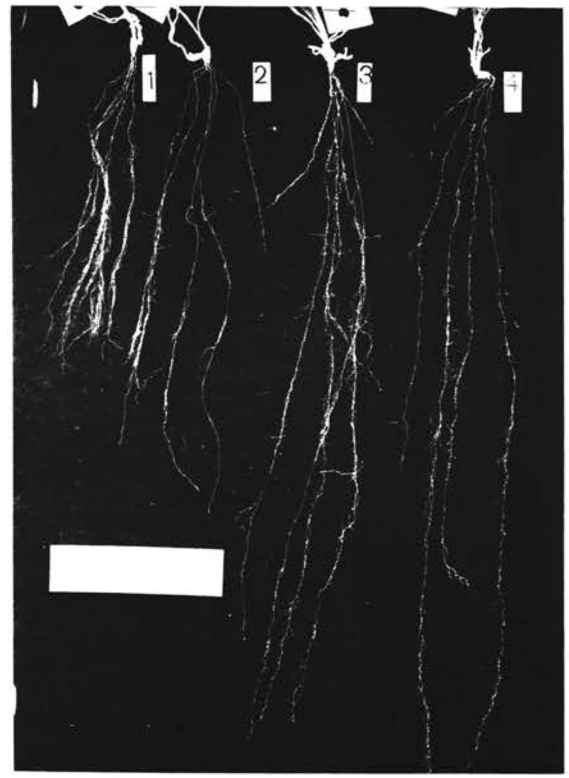
(1) Significant differences between the two species and among moisture levels exist at 1% level.
S.E.M. = 76.2 — Among moisture levels S.E.M. = 108
L.S.D. 1% = 755 mm. — L.S.D. 1% = 330 mm.
L.S.D. 5% = 327 mm. — L.S.D. 5% = 235 mm.

(2) Significant differences between the two species exist at 1% level, no significant differences among moisture levels. S.E.M. = 2.6
L.S.D. 1% = 25.7 mgm.
L.S.D. 5% = 11.2 mgm.

(3) No significant differences between the two species but significance is detected between moisture levels at 5% level. S.E.M. = 13.3 mgm.
L.S.D. 1% = 41.4 mgm.
L.S.D. 5% = 29.3 mgm.



Oats



Barley

Figure 8. Root penetration of Wintok oats and Rogers barley into soil at four different moisture levels. Moisture content of the soil increases from left to right. (See text).

TABLE XIII

TOTAL LENGTH AND DRY WEIGHTS OF THE FOLIAGE OF OATS AND BARLEY AT FOUR DIFFERENT MOISTURE LEVELS
(Averages of Three Plants)

	Wintok Oats					Rogers Barley				
Moisture Levels	I	II	III	IV	Av.	I	II	III	IV	Av.
Total length of leaves mm.	582	409	389	673	573	428	349	583	346	426
Dry weight of tops mgm.	99.8	59.2	69.2	124.2	88.1	85.3	66.2	120	92.8	91.3
Dry weight ratio of tops to roots	0.90	0.89	0.80	0.88	0.87	0.73	0.79	0.96	0.65	0.78

later when 3/4 of the oat plants were completely wilted. The recovery was very limited, and only one plant out of four in each treatment (two oat plants in treatment I) showed some renewed root activity.

It seems that only those plants which had most of their laterals growing where the water happened to reach could show some recovery. It may be noted that most of the oats in the last days of the experiment had their leaves rolled up while most of the barleys showed complete wilting, with or without leaf folding.

Observation Tests on Grasses

Penetration of plant roots into soil dried to below the wilting percentage was clearly demonstrated by the two grasses "side oats grama" (Bouteloua curtipendula Torr.) and "sand love grass" (Eragrostis trichodes Nash.).

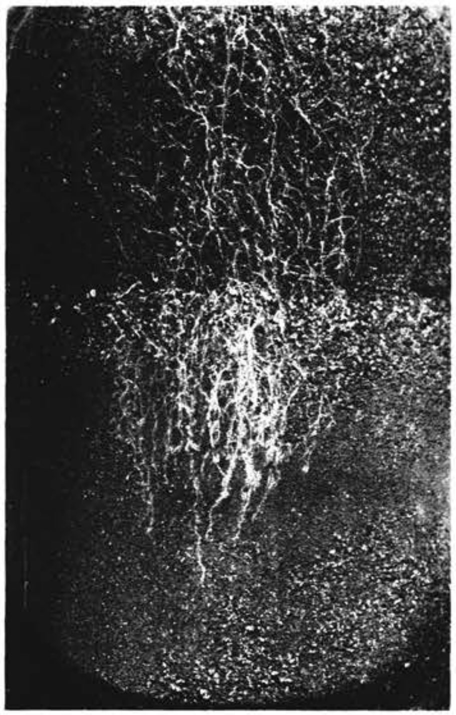
The moisture content in the bottom soil was 2.3% at the outset (estimated wilting percentage was 3.89%) while the top soil was watered to just below field capacity. Germination was normal and was complete in both the two grasses two days after sowing. Root growth in the "top soil" was relatively extensive compared to the foliage growth. It averaged 2 and 5 mm. per day for love grass and side oats grama, respectively.

Growth slowed down considerably ten days after germination, and no root growth was recorded. The general condition of the seedlings was poor in both the grasses. The leaves were short, rolled up, and looked lifeless.

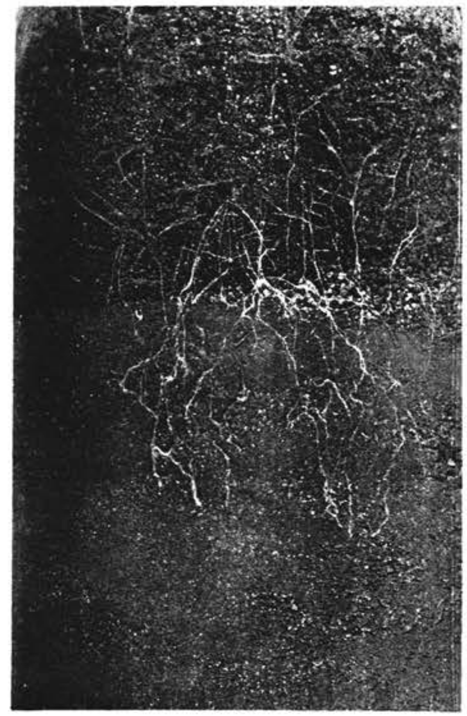
On the seventeenth day after germination water was added to the "top soil" (25 cc.) to bring it to near the field capacity. Recovery in both was remarkable. Within twenty-four hours the leaves opened up and the vivid green color was restored. Crown roots developed, but root growth went on very slowly. Laterals were more dense and more abundant in love grass than in side oats grama. In the former, the whole bunch of the roots seemed to advance into the dry soil in a "common front"; whereas in the latter, individual roots penetrated to different depths. Rate of root growth measured as mm. per day was as follows:

	In Top Soil	In Bottom Soil
Sand Love Grass	11	2
Side Oats Grama	9	1$^-$

At six weeks of age, the total average penetration for love grass was 7 cms. in the "bottom layer" as compared with 8 cms. growth in the "top layer"; and for side oats grama 5 cms. in the "bottom soil" as compared with 8 cms. in the "top soil" (Fig. 9).



Sand love grass (Era-
grostis trichodes Nash.)



Side oats grama (Bout-
eloua curtipendula Torr.)

Figure 9. Grass roots penetration into "bottom soil" below the wilting percentage.

After taking the pictures, the plants were left in the greenhouse for further observation and no water was given. The roots finally reached the bottom of the jars in both cases, and in the case of love grass, some roots started bending up again (Fig. 10). Rate of root growth then was estimated to be 2.4 and 2.8 mm. per day for side oats grama and love grass, respectively[8].

The roots in side oats grama were thicker with fewer laterals and generally shorter than in love grass which exhibited a whole mass of fine multilaterals, and which attained in general a longer system. (Fig. 9).

The moisture content of the soil upon removal of the plants on the 15th of June was 5.2% in top soil for both grasses and 2.07% in "bottom soil" for side oats grama, and 2.70% for sand love grass.

8/ Note: The relative humidity of the greenhouse after the 12th of May was very high.

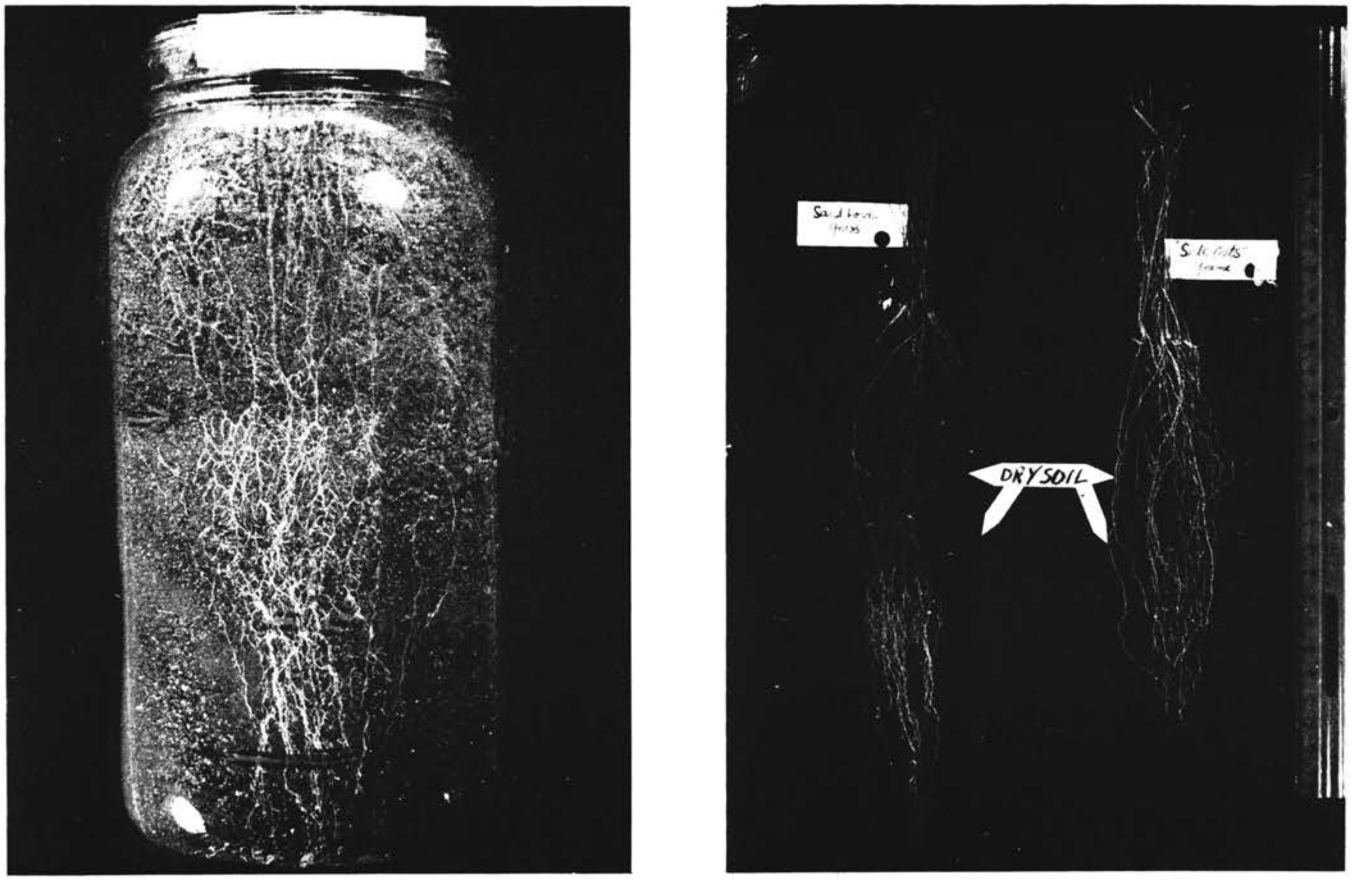


Figure 10. Grass roots penetration into "bottom soil" five weeks later than those shown in Figure 9. Left: Roots of sand love grass growing deep into the "bottom" dry soil. Right: Roots of both side oats grama and sand love grass after extracting from the soil.

DISCUSSION

Glass-fronted Observation Boxes

Root development as observed through glass in the observation boxes described above (Fig. 1) portray a relatively true picture of the actual root growth pattern under the conditions of the experiment.

Close correlation (r=.92) exists between the number of roots observed through the glass, and the actual numbers counted after digging the plants out. A similar highly significant correlation (r=.85) also exists between the total root lengths of the main root system as measured through glass and the actual lengths measured after removal of the plants from the boxes.

The use of a single plant per box was supported by Pavlychenko and Harrington (55) who maintained that studies on individual plants grown separately without competition is of value in furnishing a clear cut picture of the mode of penetration and development of the root system of each species.

The effect of light on the root areas was reduced to a minimum by keeping the boxes insulated and opening them only for a short period every day for record taking. Rogers (63) found that a short exposure to the light was of no practical importance.

The growth of the roots against the glass could also be considered not of any significant effect on the pattern of root development, and roots seemed to grow undisturbed, or as Rogers (62) noted that "the growth of the root against glass forms no serious drawback, as a pane of glass is really like a large smooth flint or grain of sand."

Roots in Relation to Soil Moisture

In all the experiments, root growth started before the leaves unfolded. Its activity as measured by the daily growth rate was at a maximum during that early stage. A definite decrease in root elongation took place upon the emergence of the first leaf, as illustrated in the summary Table XIV.

TABLE XIV

AVERAGE DAILY GROWTH OF ROOTS BEFORE EMERGENCE OF FIRST LEAF, AND DURING THE WHOLE PERIOD OF GROWTH MM./DAY

	Growth Rate Before Emergence of 1st Leaf			Growth Rate During Whole Growth Period		
Experiment	1st	2nd	3rd	1st	2nd	3rd
Wheat	23.4	32.3	-----	20.5	28.7	----
Barley	24.4	33.8	125.5	17.8	23.3	35.8
Oats	16.9	27.5	52.8	17.5	23.2	35.8

Under conditions of high moisture stress, root growth seems to come to a stop much before shoot growth ceases (Tables II, VIII). This appears to be in conflict with the conclusions reported by Rogers (62) as a result of his work on fruit tree roots, where he found that root growth continued after shoot growth ceased. In fact, it was only in the first experiment, where most roots grew in more favorable "top" layers, that root growth persisted a few days after shoot activity ceased, and only in a few plants.

During the early stages of growth the root systems of wheat, barley, and oats presented a characteristic differentiation in the number of main roots (Tables I, V, VIII, and IX), their daily growth rate (Table IX) and their spreading habits (P. 33). This is in agreement with the findings of many investigators like Weaver et al. (86, 87), Pavlychenko (54), Toumey (75), and Jamison (33). Another differentiating character between the main root systems is the color of the main roots. About 10 days after germination the color of the main roots turned yellowish in the oats, but remained white in the barley, and little affected in the wheat. The relative thickness of the main roots presented also some species differences (qualitatively). The thickest roots were found in barley, the thinnest in oats, while the wheat was intermediate. However, no definite varietal trend could be detected in all the above characters. A possible reason for lack of a definite varietal trend may be due to the small number of individuals (plants used as experimental units) used, and to the presence of a large amount of variation among individual plants within the same variety, thus increasing the experimental error and decreasing the sensitivity of the test. Many workers, however, have reported on the existence of varietal differences in the root system based on general observations rather than replicated trials [Worzella (89), Walworth (79), Aamodt and Johnson (1), Cook (17), and Derick and Hamilton (20).].

Root growth in the bottom layer, did not proceed in any definite pattern in the first experiment, and in fact did not take place except in two or three plants. The reason may be that by the time the roots reached the "bottom" layer, most of the moisture content in the "top" layer was exhausted due to its depth, which left the whole root system in a rather poor condition. In the second experiment, on the other hand, with its shallow "top" layer (15 cms.), the roots were in contact with the "bottom" layer at an earlier stage (Table VII). Barley was the first to reach the "bottom" layer (average 3.8 days), then came the wheat (average 4.3 days) and the last was the oats (average 6.1 days). It is also of interest to note that in the second experiment, the activity of the roots in the dry layer persisted for 2.4 days in the case of barley, 1.2 days for wheat, and 1.1 days for oats. Total penetration as presented in Table VIII shows also this species trend, but no varietal differences could be detected.

On the whole the seminal root system, to which Pavlychenko (54) attributes variations in the early development of cereals, presents a definite increase in the barley over either oats or wheat (Table VIII). The crown roots, on the other hand, did not develop except after watering in the first experiment; while conditions were too dry for them to develop in the second experiment. Their total length and number in the oats were less than in the barley or wheat during the first twenty-five days of growth (Table VI), but they exhibited a rather fast growth pattern after that period and attained finally as much length as in barley or wheat. Pavlychenko (54) reported higher figures for barley, than wheat or oats. Although the figures presented in Table VIII did not show such superiority, barley would be expected to yield a larger root system had they been growing in a broader container as many crown roots, growing laterally outward, hit the sides of the containers and stopped any further growth, whereas wheat or oats roots followed a downward path.

Lateral root spread could not be measured through the glass, as most of the laterals seem to grow inside the soil mass, and only portions showed out through the glass fronts. Dry weight records have, therefore, been used to indicate the relative root mass to a certain depth in the soil (Weaver et al. 84).

Differences among species were also demonstrated in the dry weights of the roots as shown in Tables V, VI, VIII, and XII, but no definite varietal trends were detected.

The ratio of dry weight of tops/roots which was used by such early workers as Harris (26) as a guide for root and soil moisture relations, provides an interesting index. Barley shows the lowest figures indicating a smaller shoot and a relatively larger root system than the two other species (Table V) in the first experiment, while in the second, the ratios for barley and wheat were the same and both were lower than oats. Generally under the conditions of the second experiment, more roots were produced in barley than in wheat and more in wheat than in oats (Table VIII).

Soil Moisture and Root Development

As can be seen from Figures 2-5 and also from Tables IX and XI, the average daily growth rate of the roots decreased gradually and in proportion with the decrease in the soil moisture content. Table IX shows an average daily increase of 43 mm. and 126 mm. for oats and barley respectively in the "top layer" and during the first four days when the soil moisture tension was in the neighborhood of 1/3 atm. The average daily growth, however, decreased in relation to the soil moisture level as presented in Table XI and more clearly in Figure 11.

The decline in growth is continuous as soil moisture is actually being lost through the growing plants and some (expected to be very little) through surface evaporation - Figures 2-4.

The data obtained from the third experiment show that the root activity came to a stop in the higher moisture tension treatments at an earlier date than in those with lower moisture tension (Fig. 11) and Table XI). The moisture content of the soil at that stage is presented in Table XV.

TABLE XV

MOISTURE CONTENT OF "TOP" AND "BOTTOM" SOIL BEFORE AND AFTER CONDUCTING THE EXPERIMENT

(Third Experiment)

Treatment	Moisture Content at the Beginning	Moisture Content at the End		Loss of Moisture Content	
		Barley	Oats	Barley	Oats
I	4.3%	1.47%	2.15%	2.83%	2.15%
II	5.1%	1.91%	2.43%	3.19%	2.67%
III	8.1%	2.84%	3.28%	5.26%	4.82%
IV	10.5%	4.08%	4.73%	6.42%	5.77%
Top Soil	17.4%	2.2%		15.2%	

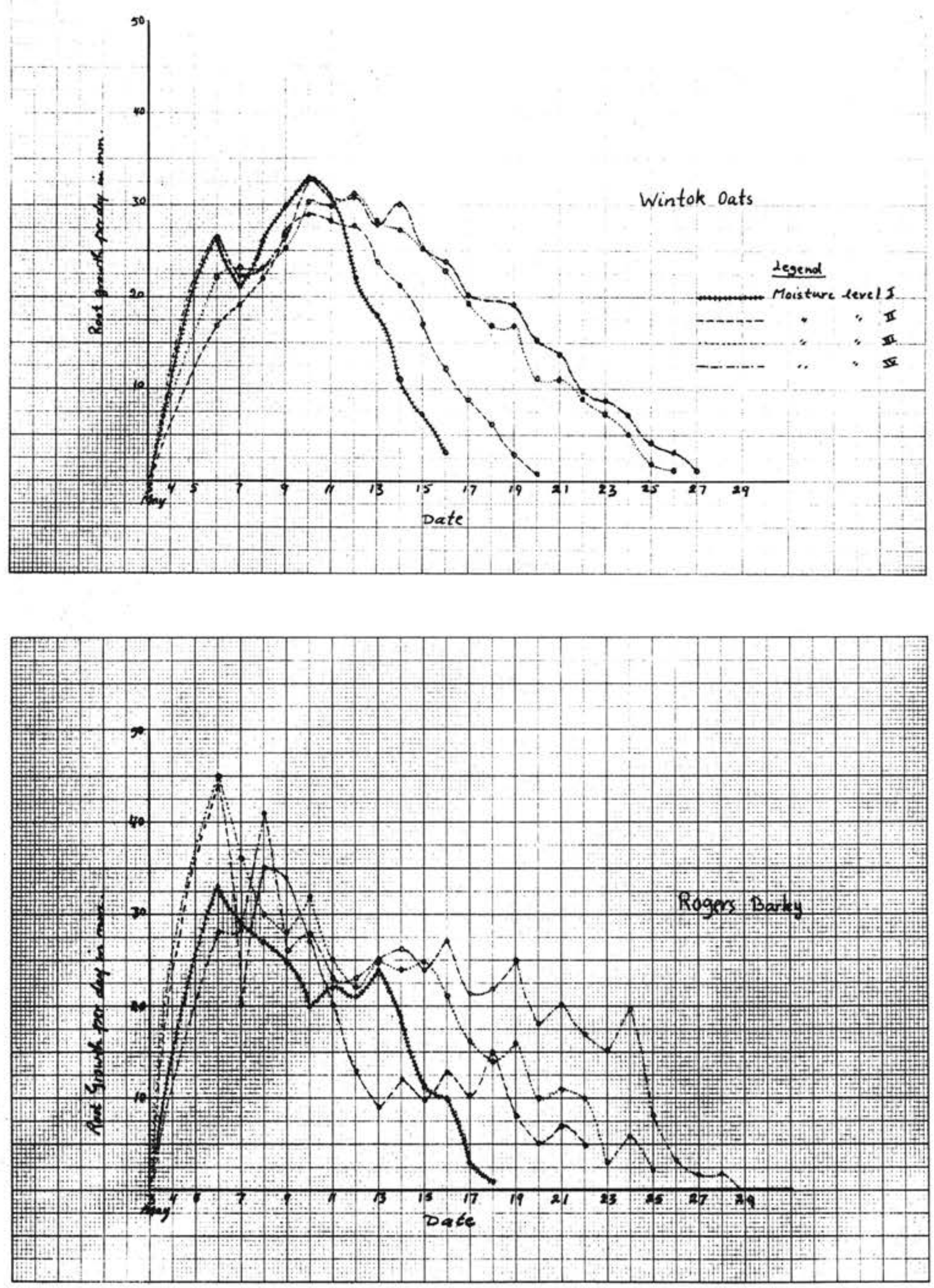


Figure 11. Average daily growth rate of the roots of oats and barley in each of the four moisture levels. (Third experiment).

Thus it is clear that the lower the moisture level the less moisture is available to the plants that can be extracted. Actually a decrease to 36% of the original moisture level was effected by the barley, and to about 55% by the oats in all treatments. This relation can best be shown by a graph (Fig. 12).

Thus it is clear that barley causes a greater loss of soil moisture than oats, which may present a reason why oats continued growth activity and showed delayed wilting as compared with barley (P. 55).

The fact that oats reduced soil moisture less than barley conflicts with the findings of Weaver et al. (84) where it was stated that oats reduced soil moisture more than wheat or barley.

The decrease in root growth as a result of the decreased moisture content of the soil has also been reported by many workers like Gingrich (23), Jamison (33), Rogers (62) and Richards and Wadleigh (60). The latter emphasized that the decrease in growth occurs at quite low stress levels, which agrees with the present study as indicated in Figures 2-4 where reduction occurred after the first 3 to 4 days after germination. Actually as the soil moisture content decreases, the moisture tension increases to a greater extent (Appendix 1) and thus the soil moisture becomes less and less available to the plant. This in turn would decrease the hydration of the plant cells and consequently decrease the turgor pressure in those cells. Slatyer (70) presented a favorable argument in this respect.

Although other workers as reported by Veihmeyer and Hendrickson (76) presented contradictory evidence as a result of work on a variety of plants, and

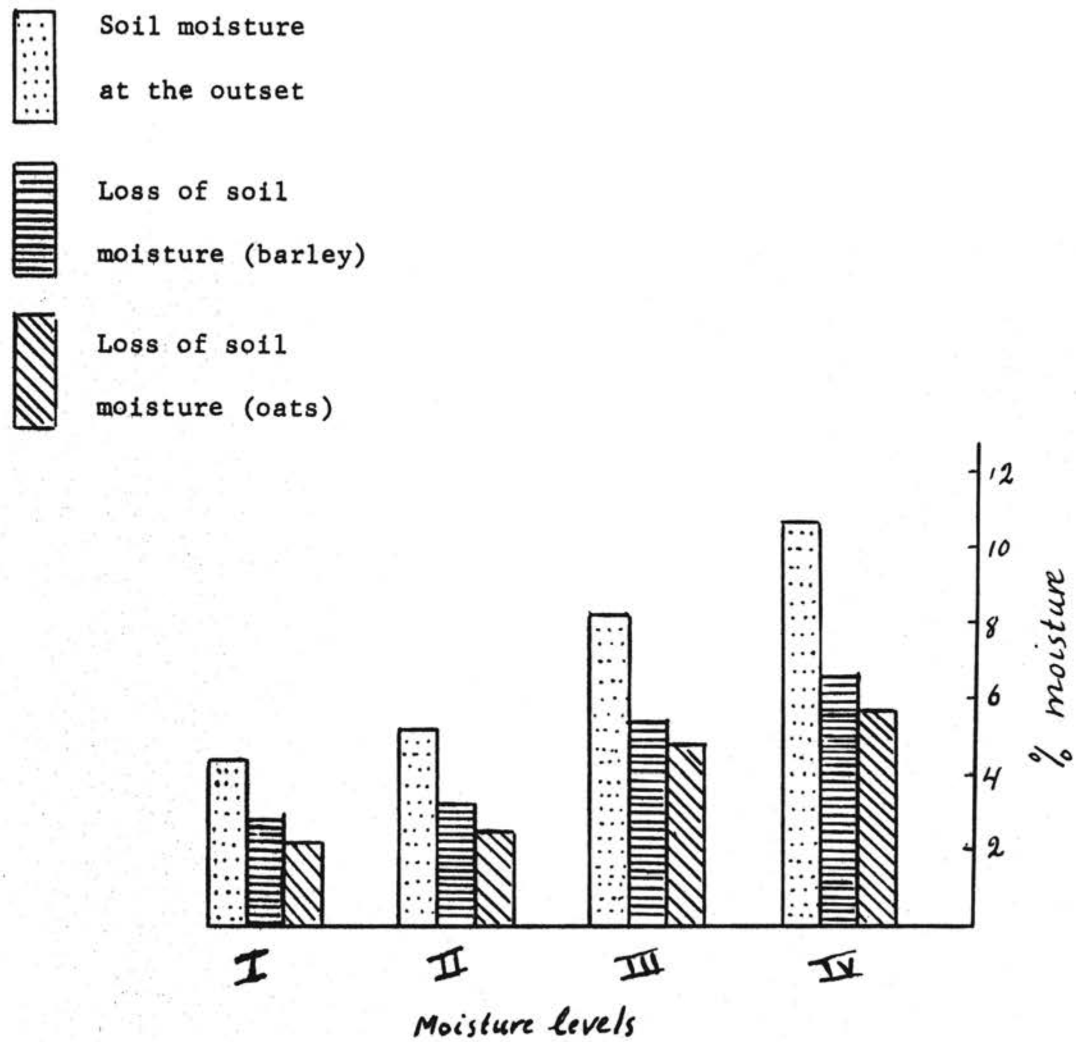


Figure 12. Effectiveness of oats and barley in reducing soil moisture level. (Third experiment).

held the view that water was equally available to plants throughout the range from field capacity to wilting percentage, the present study is actually in favor of the former view that water is not equally available to plant growth throughout the above range and consequently as soil moisture tension increases, growth rate decreases.

The relationship between growth and soil moisture is illustrated in Table XI which shows a decrease in the number of days of active growth with increased soil moisture tension, coupled with a reduction of the daily root growth rate. Figures 7, 8, and 11 also illustrate this.

Root activity in the first experiment came to a stop in seven eighths of the wheat plants, half the barley plants and three quarters of the oat plants (Table II) when the moisture content in the "top" layer reached 6.27% and in the "bottom" layer 1.59%. At this stage, however, some shoot activity continued in all the wheat plants, and in three quarters of the barleys and oats. It may be that, in accordance with the remarks by Briggs et al. (12) and Kramer (38) where they mention that a steady loss of soil moisture goes on even after the death of the plants, and that plants can reduce the moisture content far below the wilting percentage, the little moisture absorbed from the soil helped the top foliage to remain alive and maintain some growth activity. Breazeale and Crider (11) reported on the ability of roots to absorb a limited amount of plant food from dry soils at the wilting percentage, under conditions of humid atmosphere. In the present experiments the atmosphere was more humid during the third experiment where a similar phenomenon was noticed.

Recovery of wilted plants after irrigation, used by some workers as an index for detecting drought tolerant plants (32), did not show any definite trend in the present series of experiments. This may be due to the fact that when watered, not all plants were wilted to the same extent. In fact some were reported dead or in a very poor condition such that recovery was not likely to occur. It is in my opinion that a specially designed test should be conducted if this point needs to be studied further.

Root Penetration and Extension in Dry Soil

No penetration of significance was recorded in the first experiment, probably due to the depth of the more favorable "top soil" (see P. 29). The moisture content of this top layer dropped from 11.49% to 6.27% (wilting percentage = 6.44%) when all plants showed some degree of wilting. After wilting, however, activity was mainly centered in the formation and growth of new crown roots; whereas the old seminal roots which appeared to have stopped functioning, were thin and appeared dull colored especially in oats and wheat.

Under the more severe conditions of the second experiment, on the other hand, some root penetration took place into the dry soil which had a moisture content of 2.3% (wilting percentage = 3.89%). The barley roots penetrated most, followed by wheat and then oats. Penetration in soil at different moisture levels as measured in the third experiment provided an interesting quantitative study concerning the extent and depth of penetration (Table X). The depth of root penetration was directly proportional to the soil moisture content (Figs. 7 and 8).

This is in agreement with the findings of Weaver et al. (86).

The extent of the whole root system, including lateral growth, however, presented a different pattern. It was noticed especially in the lowest moisture treatment I, that lateral growth tended to concentrate in the region separating the top and the bottom layer. This is clearly seen in the high dry weight of the top 15 cms. of the whole root system in treatment I in both barley and oats (Table XII). This supports the hypothesis that relatively dry conditions induce more branching as reported by Kmoch (37) and Weaver et al. (86) who differentiated between the extent of root growth under dry conditions and that under heavy irrigation where more depth of penetration and a larger mass of roots were produced. The present experiment indicates that favorable moisture conditions induce root elongation through the moist layer, whereas dry conditions seem to cause more lateral spread and less penetration. Breazeale and Crider (11) concluded from a split-root experiment on orange plants that more roots were produced in moist soil than in dry soil. This tendency was found to occur in the higher moisture treatments II, III, and IV (Table XII) where higher dry weights were recorded for the lower moisture tension levels in the "bottom soil".

The root penetration into soil below the wilting percentage was clearly demonstrated by the grass observation test (P. 55). Figures 9 and 10 show the extensive and almost uninterrupted root penetration into the bottom soil which had a moisture content of 2.3% at the beginning (wilting percentage = 3.89%) and 2.07% and 2.78% for side oats grama and sand love grass respectively at the termination of the experiment.

The suggestion of Breazeale et al. (9) that leaves can act as absorbing organs and transport moisture under humid atmosphere, may have some bearing on the above observation on the large extent of the root system of the two grasses in question into soil below the wilting percentage. The atmosphere in the green-house during the test was quite humid but not as humid as that to which Breazeale referred. This, however, has to be further tested for this observation to be verified. Penetration into the dry soil by the two known drought resistant grass strains is a further proof in favor of the argument that the roots of the drought resistant strains possess the ability to grow into soil below the wilting percentage as presented by Shantz (66) and Magistadt and Breazeale (44) and contradicts the reports of Hendrickson and Veihmeyer (28).

It may be added that such a characteristic i.e. the ability of the roots to penetrate dry soil is more of a species character rather than a varietal behavior, and that humid atmosphere seems to favor such penetration.

SUMMARY AND CONCLUSIONS

Three sets of experiments were carried out in the Botany greenhouse of the Oklahoma State University at Stillwater between February 1962 and May 1962. The purpose was to study the behavior of the root systems of each of two varieties of wheat, barley and oats under conditions of soil moisture stress, and thereby to determine any relationship that may exist between the root systems and drought tolerance.

Specially designed glass-fronted, portable wooden boxes were used, each contained a single plant.

A randomized block with a split plot arrangement was used for the tests which contained two varieties of each of the three species and a fixed soil moisture content at the outset in the first and second experiments. The third experiment consisted of four moisture levels for each of two varieties only, one of oats and one of barley. In all the experiments, each box was filled with two layers of soil to various depths. The "top layer" was started at or near field capacity while the "bottom layer" was subjected to the moisture stress.

In addition, an observation test on the ability of roots to penetrate dry soil below the wilting percentage was carried out using two known drought resistant grass strains, namely sand love grass (*Eragrostis trichodes* Nash.) and side oats grama (*Bouteloua curtipendula* Torr.). The grasses were sown in wide mouthed 3" glass jars.

The results emphasized the presence of characteristic differences among the three cereal species, but no varietal differences of significance were detected within any one species. Barley seemed to possess the largest number of roots and the greatest total length as well as the highest dry weight and the widest lateral spread. Next was the wheat, then the oats.

Root and shoot growth were found to be proportional to the available soil moisture, and growth decreased gradually as the soil moisture content was decreased until it stopped at or nearly at the wilting percentage. In most cases root growth stopped a few days before shoot growth which, however, was maintained at a much reduced rate.

Root penetration into dry soil and total length of the main roots were directly proportional to the soil moisture content. Lateral spread and branching as measured by dry weights seemed to be induced by dry conditions which at the same time limited root elongation.

Barley appeared to reduce the soil moisture content to a greater extent than oats and it actually showed signs of wilting earlier than oats.

Penetration of roots into soil below the wilting percentage was clearly demonstrated by the two grass strains used. The growth of their roots into the dry layer was extensive and seemed to go on with no apparent interruption but at a very slow rate. Absorption of moisture from the atmosphere by the foliage is, however, suspected.

It is concluded that the glass fronted boxes used are useful for root studies during the early stages of growth. Root penetration into dry soil below the wilting percentage is exhibited by drought resistant species, and that in the present study no significant varietal differences in this respect were found.

Due to the presence of great variation among individual plants, a larger number of replicates and experimental units may give a more sensitive test of the characters that were studied. It may be suggested that a similar study under controlled atmospheric conditions, and if possible, fixed soil moisture content, may yield more information.

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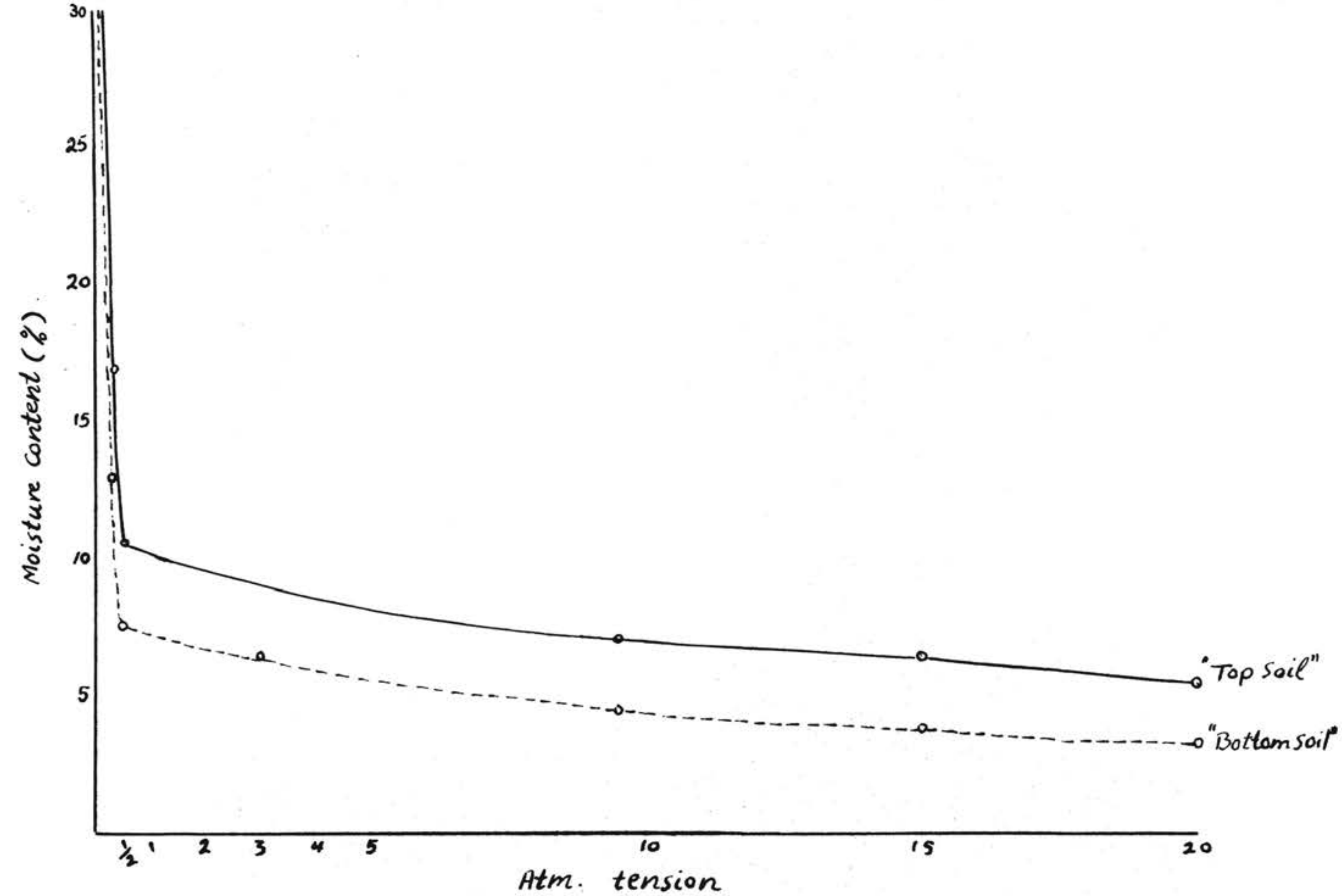
APPENDIX



Appendix Figure 1. Relationship between soil moisture content and soil moisture tension.

VITA

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