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John Ernest Weaver, Joseph Kramer, Maud Reed

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J. E. Weaver
University of Nebraska-Lincoln

Joseph Kramer
University of Nebraska-Lincoln

Maud Reed
University of Nebraska-Lincoln

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DEVELOPMENT OF ROOT AND SHOOT OF WINTER WHEAT UNDER FIELD ENVIRONMENT

J. E. Weaver, Joseph Kramer, and Maud Reed
University of Nebraska

Numerous studies have been made on the winter killing of cereals, but few data are available on their actual growth rates during fall, winter, and early spring. No attempt has been made to correlate growth with environmental conditions, at least in the great wheat belt of the Mississippi Valley and Great Plains. During the fall of 1921 a study of the development of winter wheat both above and below ground was begun. A strain of Turkey Red winter wheat recently developed at the Kansas Agricultural College and known as Kanred was grown.

A plat of one tenth acre of fertile silt-loam soil was secured in the city of Lincoln. It was conveniently located near the University of Nebraska where living plants could be easily transferred for careful study to the laboratories of the department of botany. The field had been formed by breaking the native sod four years previously, and four crops had been grown. The 1921 crop was corn which had been cut during the latter part of August. The soil, which was in excellent tilth, was plowed to a depth of about four inches on September 20 and repeatedly harrowed until a good seed bed was obtained. The wheat was immediately drilled at a depth of 1.5 to 2 inches, the rate being 75 pounds per acre. Immediately before plowing, all stubble and weeds were removed in order to prevent them from interfering later with root excavations.

A Friez's hygrothermograph and a number of soil thermographs were placed in appropriate shelters in the field. The hygrothermograph was placed in such a manner that the mechanisms sensitized to humidity and temperature changes, respectively, were about four inches above the soil surface. A continuous record of soil temperature was secured at depths of three and eight inches. These instruments were checked frequently, and the humidities and temperatures averaged in five-day periods as follows: The averages for the day temperatures (or humidities) were found by adding the temperature at 8 A.M. and every two hours thereafter until 6 P.M. for each day and dividing the sum by the total number of two-hour intervals. Those for night temperatures were calculated in a similar manner beginning at 8 P.M. and including the readings until 6 A.M.

Ten days after planting a study of the shoot and root development was begun, and was repeated at ten-day intervals until November 1, after which the interval between examinations was extended to fifteen days or more. At

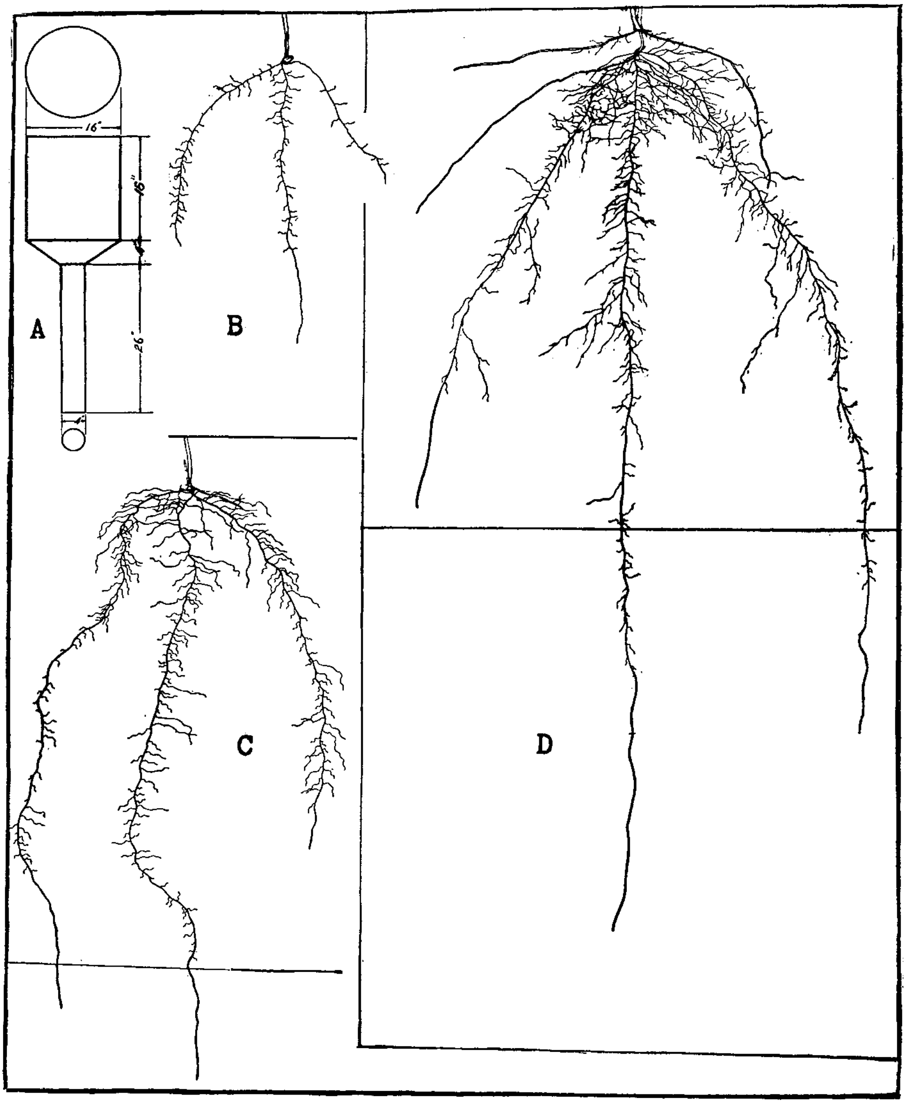

FIG. 1. A. Container in which wheat was grown in the field for root area determinations.

B. Primary root system of 10-day-old winter wheat plant (Sept. 30).

C. Plant 20 days old. The first root of the secondary system has appeared.

D. Roots of 30-day-old plant. The secondary root system now furnishes 18 per cent of the absorbing area, which is 62 sq. cm.

The two squares on the right represent square feet. All root systems are drawn to the same scale.

each examination, until November 29, the area of the above-ground parts was determined by means of solio prints and a planimeter. In making the prints the leaves were cut at the ligule, or, if only partly out, where they emerged from the sheath, and were carefully flattened out for printing. The area of the short stems was calculated from the surfaces obtained by flattening the stems in the printing frame. The photosynthetic area was determined on about 25 plants selected from different portions of the field to represent average conditions.

Growth, as indicated by the dry weight of the plants exclusive of roots, was also determined at the end of each period. Plants were secured from ten different portions of the plat, carefully selected as representative of the field as a whole. From this lot of material 100 to 150 medium-sized plants were selected for determination of dry weight. Before weighing the plants, but while they were kept in a moist condition, measurements of leaf dimensions and counts of the number of tillers were made. The plants were placed in open moist-chambers, so that they quickly became dried in an oven at 70° C., after which they were transferred to weighing bottles and kept at 100° C. until thoroughly dry. They were then cooled in a desiccator and the dry weight ascertained.

The root development was studied by digging trenches in such a manner that the perpendicular walls containing the plants to be examined could be undercut and the soil carefully removed by means of a specially designed handpick and other appropriate apparatus. In this manner the root systems of many plants were secured in their entirety.

The absorbing area of the roots was obtained for plants grown under similar conditions as regards soil, time of planting, etc., during the fall of 1922. For these experiments containers of especial design were used, which afforded sufficient room for normal root development without requiring an excess of soil to be removed in recovering the roots. They were made of galvanized iron and consisted of a cylindrical top with sloping bottom which opened into a long cylindrical base of small diameter (fig. 1A). The sizes of the containers were progressively increased to accommodate plants of greater age and development. The largest containers, which were removed November 14 and 29, were 16 inches in diameter at the top and 18 inches deep, while the lower portion, which accommodated the deeper primary root system, extended to a total depth of 4 feet and had a diameter of 5 inches. The containers were filled with rich loam soil, well screened and mixed with about one fourth sand, which had an available water-content of approximately 20 per cent. This afforded a sufficient supply throughout the experiment. The deeper portion of the larger containers was filled with subsoil similarly prepared. After filling, the containers were placed in the soil in such a manner that the level of the tops, which were covered with black oilcloth to retard evaporation, was slightly above that of the general soil surface. Four plants were allowed to grow in each container through an opening three inches in diameter in the center of the oilcloth cover. Wheat was sown about the containers, and thus field conditions rather effectually established.

Certain containers were removed at the end of each ten-day period and the photosynthetic area and root area determined. The roots were carefully removed from the soil, after cutting away the container, and placed in large flat pans of water where they could be freed from practically all the larger soil particles with little or no injury to the root. To successfully separate the roots from the soil it is very essential that the latter be of the proper texture, water-content, and compactness. Considerable experience as well as patience is also required. When the root system became more complex, owing to the greater number and length of fine laterals, it was found expedient to recover it by means of washing. This was done very slowly with a fine spray and rather low pressure to avoid breaking the roots. Ordinarily three or four hours were required for a single operation. It was found necessary to support the soil mass on the bottom and sides of the container, an opening down one side being cut to permit the use of the spray. Thus the root system was secured almost if not completely intact. By letting the muddy water filter through a 2 mm. mesh screen the very few broken fragments were all recovered. Black paper was placed on the bottoms of trays of water into which the washed roots were transferred. Here they were floated out into their natural position (as previously ascertained in the field) and the area measured. This was accomplished by determining the length of the main roots and their average diameters as measured by a micrometer eyepiece under a magnification of about fifty diameters. The branches were counted and their lengths and diameters measured. The process was repeated for the branches of the second order, etc. A very large number of diameter measurements were made as this dimension was found to be quite variable. The water, of course, prevented any shrinkage of the root system. From these data, which were secured only after a long tedious process from an average specimen of the four plants thus prepared, total root areas were calculated. This corresponded, unless otherwise stated, with the total absorbing area, exclusive of root hairs.

First Ten-day Period, September 20 to 30

The first ten-day period was mostly one of clear, warm days (75° F.) and cool nights (59° F.). Relative humidity averaged 57 per cent and the available soil moisture—*i.e.*, the amount above the hygroscopic coefficient—was 20 per cent in the zone of root growth. The stand was uniformly good. The plants averaged four inches in height and the second leaf was about half grown. The average photosynthetic area was 8.28 sq. cm. and the dry weight 0.013 grams.

Although the plants had been above ground only six or seven days, the primary or seminal root system was already well developed (fig. 1B).

Some variation in the number of roots occurred, from two to four not being rare, but nearly all of the plants had three. Of these one, perhaps the primary root, was deepest, extending to maximum depths of eight or nine inches. While the deeper roots mostly took a more or less directly downward course, it was usual for the others to oblique outward frequently at an angle of 30° from the soil surface, often turning downward later. They had an average lateral spread from a vertical line through the base of the plant of 2.5 inches, while the maximum spread was four inches. The working depth, or average depth of the general absorbing level, was six inches. The roots were fairly well furnished with laterals ranging from 1 to 25 mm. in length, relatively few exceeding 15 mm. Often the laterals were scattered irregularly, the best branched portions giving rise to twelve or more rootlets per inch. On some roots they occurred nearly to the tip, on others the rapidly growing tips were free from rootlets for distances of 0.5 to 2 inches.

In 1922, an average root area of 9.63 sq. cm. was found ten days after planting. This was slightly greater than the photosynthetic area, which was 7.68 sq. cm.

Second Ten-day Period, October 1 to 10

During the second period the crop made an excellent growth. Clear, warm weather continued, with average day and night temperatures of 68° F. and 50° F. respectively. The relative humidity averaged 50 per cent, but only 35 per cent during the day. The soil was warm (64° F.), with plenty of available water (14 per cent), conditions very favorable for root growth. The plants had reached an average height of 5.5 inches. The average number of leaves was 4, although some plants had as many as 6. Tillering had begun. Nearly all of the plants had one tiller which extended an inch or two from the axil of the first leaf. These leaves were rapidly loosing their vertical

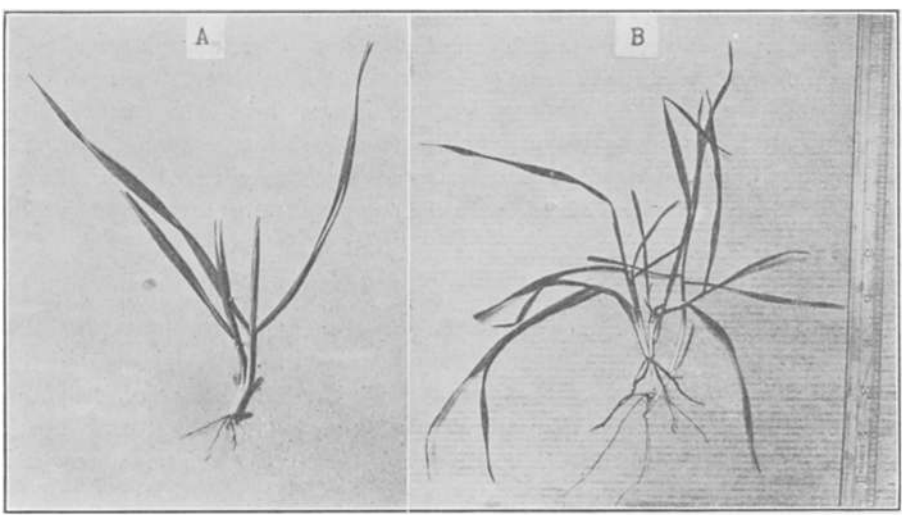

Fig. 2. A. Winter wheat 20 days old.
B. Winter wheat 30 days old. Note the abundance of tillers.

position, some already being nearly horizontal. A second tiller originating either from the axil of the second leaf or more commonly from near the grain within a sheath, was found on most plants, while on others a third tiller was in evidence (fig. 2A). Where the seed was deeply planted tillering was not so far advanced. The total leaf area had nearly tripled (21.5 sq. cm.), while dry weight had increased from 0.013 to 0.046 grams.

Of 34 plants excavated for root examination, 4 had two roots in addition to the primary root system, 20 had one, while 10 plants showed no beginnings of a secondary root system (fig. IC).

These roots of the secondary system were about a mm. thick, turgid, white, and entirely unbranched, but densely clothed with root hairs (cf. Brenchley and Jackson, 1921, and Jackson, 1922). Originating from the stem near the grain, they ran off mostly in a horizontal position or turned only a little downward. They varied in length from only a sixteenth of an inch to 2.5, 0.7 inch being an average. Where the grain was deeply planted the secondary root system was beginning to appear at the swollen node about an inch below the soil surface. The roots of the primary system had continued their downward growth, none extending laterally more than 6 inches from the base of the plant, although this spread was often reached at a depth of only 3 or 4 inches. The average lateral spread was 4 inches. The working depth had been increased at the rate of about 0.5 inch a day and now reached 11 inches; a maximum penetration of 15.5 inches was recorded. As at the preceding examination, the lateral rootlets occurred irregularly. Sometimes an inch of root would have few or no branches, while again as many as 15 might occur. As a whole the roots were more frequently branched and the branches were longer than before, especially in the first 6 inches of soil. No secondary branches occurred. In general the laterals on the deeper roots (below 8 inches) were scarce and short. Usually the thick, shining white, rapidly growing root-ends were destitute of laterals for a distance of 3 to 5 inches back from the tip.

The leaf area of plants of similar age grown in 1922 was approximately that of the preceding year, 22.5 sq. cm., and the absorbing surface of the roots was 31.39 sq. cm., which was approximately a third larger than the surface of the above-ground parts.

Third Ten-day Period, October 10 to 20

During the following period of clear, dry, warm weather the crop made a remarkable growth. The average day and night temperatures were 66° and 51° F. respectively; the average daily humidity 48 per cent, that for the day being only 37 per cent; the soil at both 3 and 8 inches depth had an average temperature of 61° F.; while the available water-content in the zone of root growth was 6 to 14 per cent. The great increase in photosynthetic area, from 21.5 to 59.5 sq. cm., made possible the correspondingly large increase in dry weight, from 0.046 to 0.146 g. Owing to the abundant tillering from the axils of the leaves, and the consequent spreading and more or less horizontal position of the latter, the plants had decreased in average height from 5.5 to 3.5 inches. The stems extended about an inch above ground. Most of the parent plants had the fifth leaf about half developed, while a maximum of

TABLE I. *Water-content of soil in excess of hygroscopic coefficient*

Date	0.0 to 0.5 Foot	0.5 to 1.0 Foot	1 to 2 Feet	2 to 3 Feet
	per cent	per cent	per cent	per cent
Sept. 20	22.0	25.5	15.8	....
Sept. 30	18.0	18.8	11.8	....
Oct. 10	10.5	14.4	5.7	5.7
Oct. 20	6.7	11.5	5.7	3.1
Oct. 30	10.2	15.4	8.0	....
Nov. 14	10.5	9.5	6.5	....
Nov. 29	9.0	12.7	8.0	6.9
Dec. 14	6.0	10.4	6.7	6.5
Jan. 13	10.5	9.6	4.7	4.7
Feb. 12	19.2	11.8	5.0	6.3
Mar. 14	14.0	14.8	6.7	8.9
Mar. 24	19.5	17.8	7.0	....
Hygroscopic coefficient	10.0	8.2	12.3	14.5

six leaves was found on some. All were in good condition except the oldest, which were in various stages of deterioration from yellowing at the tip to being entirely discolored and dead.

Measurements of the length and width of many leaves, made at the end of each ten-day period, were concluded at this time. The first leaves, when fully grown, averaged 98 mm. in length and 3.1 mm. in width; the second 145 mm. and 3.5 mm.; and the third 156 mm. and 5.2 mm. respectively. This progressive increase in length did not hold for the fourth leaf (148 mm.), although the width was greater (5.25 mm.) than for any of the preceding.

All of the tillers which were visible without pulling apart the leaves were counted on 50 carefully selected, representative plants. An average number of 4 tillers was obtained. This was more than twice the number that occurred on October 10. They varied in development from those just out of the leaf sheath to others with three leaves, the longest of which reached 5.5 inches. Some of the tillers stood as high as the parent plants. Not only did they occur in the axils of the third and fourth leaves, but some of the older tillers were already giving rise to new individuals. A maximum of 12 tillers was counted on some plants. A marked under development of tillers was noted in plants from deeply planted seed. At this time the prostrate habit of the crop was well initiated, the plants having an average spread of 3.5 inches on each side of the drill row (fig. 2B).

The primary roots had now reached a working level of about 1.3 feet, while maximum depths of 2.8 feet had been attained by some. Roots were found not infrequently at depths of 2 to 2.4 feet.

While all the root ends were, as before, usually unbranched, these deeper ones were also often free from laterals for distances of 6 to 10 inches from the tips. Not only had the general lateral spread of the primary roots increased 2 or 3 inches, those ending nearer the surface being most profusely branched, but the length of the laterals was also greater in the upper soil. Above 15 inches depth branching averaged about 5 to 7 laterals per inch. The average length of the branches was approximately 1.2 inches. At greater depths branches were not only less numerous (1 to 5 per inch) but also shorter. By exercising great care in their excavation and studying the roots submerged in large shallow pans of water minute details of branching habit, etc., were determined. Secondary branches on the laterals from the main roots were found only on the oldest, where they were fairly abundant.

The secondary root system had made a marked growth, so that each plant now had a total of 4 to 10 roots, including the 3 seminal ones (fig. 1D).

An average of 4 secondary roots per plant was determined. These varied from one eighth to 6 inches in length and ran off from horizontal to nearly vertically downward, not uncommonly roots 5 or 6 inches long ended at a depth of 4 inches. These fleshy new roots had usually twice the diameter (about a mm.) of the seminal ones in the surface soil, and only in the deeper layers was the diameter of the latter equal to that of these secondary roots. They were densely clothed with root hairs and in addition the larger ones had branches varying in length from .03 to .3 inch. Where the seed was deeply drilled roots originated from a node an inch below ground-line, otherwise they grew from near the grain and from the base of the tillers.

The total root area of plants of the same age, grown thus far under very similar weather conditions, was 61.51 sq. cm. This exceeded the photosynthetic area, which was 50.5 sq. cm., by about 22 per cent.

Fourth Ten-day Period, October 20 to 30

Following October 20 the weather remained dry and warm. The average day and night temperatures were 59° F. and 50° F. respectively. The soil temperature at 3 and 8 inches depth averaged 58° F. Some cloudy days occurred and enough rain (0.87 in.) fell during the last three days to renew the moisture of the soil to a depth of about 5 inches. The second six-inch layer of soil had about 13 per cent available water, but below this it was drier (7 per cent). The average relative humidity for day and night was 56 and 70 per cent respectively.

Responding to these favorable environmental conditions the crop had made an excellent growth. The photosynthetic area had increased 58 per cent (93.98 sq. cm.)and the dry weight 64 per cent (0.239 g.). Over about half of the field the plants had spread out in such a manner as more or less to cover the soil, elsewhere bare areas were in evidence (fig. 3). Although the plants averaged only 3 inches in height, the lateral spread was nearly 4 inches on each side of the row and some had a maximum spread of 6 inches. Most plants now had one or two dead leaves and on some the third leaf was more or less deteriorated, thus giving the field a slightly yellowish tinge. The parent plants had a total of 5 to 7 leaves; many of the larger tillers had 4, the fourth being only partly mature. An average of 7 tillers per plant was found. Twenty-eight per cent of the tillers had three or more leaves partly or entirely developed, 28 per cent had 2 leaves, while 44 per cent had only one. Plants of average size had at this time a total of 20 leaves, over half of which were fully developed.

An examination of the primary root system showed that it had increased a little both in working depth, to about 1.7 feet, and maximum extent, a few of the deepest roots having penetrated to 3 feet. The older portions of the roots, especially the first foot of the deeper ones, appeared shriveled, and

FIG. 3. Detail of the crop on October 30, 40 days after planting.

microscopic examination showed a deterioration of the cortex, but the abundant root hairs on both the deeper main roots and their branches, together with their bright, turgid appearance, showed plainly that they were functioning vigorously as absorbing organs.

The primary branches were longer than before (1 to 3 inches or more) and on some roots much more abundant secondary laterals varied in length from .03 to an inch. From 3 to 8 usually occurred on an inch of primary branch. Thus the efficiency of the root system was greatly increased.

Secondary roots now averaged 9 per plant. The average length per root was about 2 inches, but they varied in length from a few millimeters to 19 inches. In general they ran rather obliquely outward and downward with an average spread from the base of the plant of about 5 inches (fig. 4A).

Some of the longest obliqued downward to depths of 18 inches, while most of these thick, turgid roots even when 2 or 3 inches long often had no laterals; the older and longer ones frequently were branched at the rate of 5 to 10 laterals per inch. These occurred in very irregular groups, and although .2 to 1.5 inches long, were practically

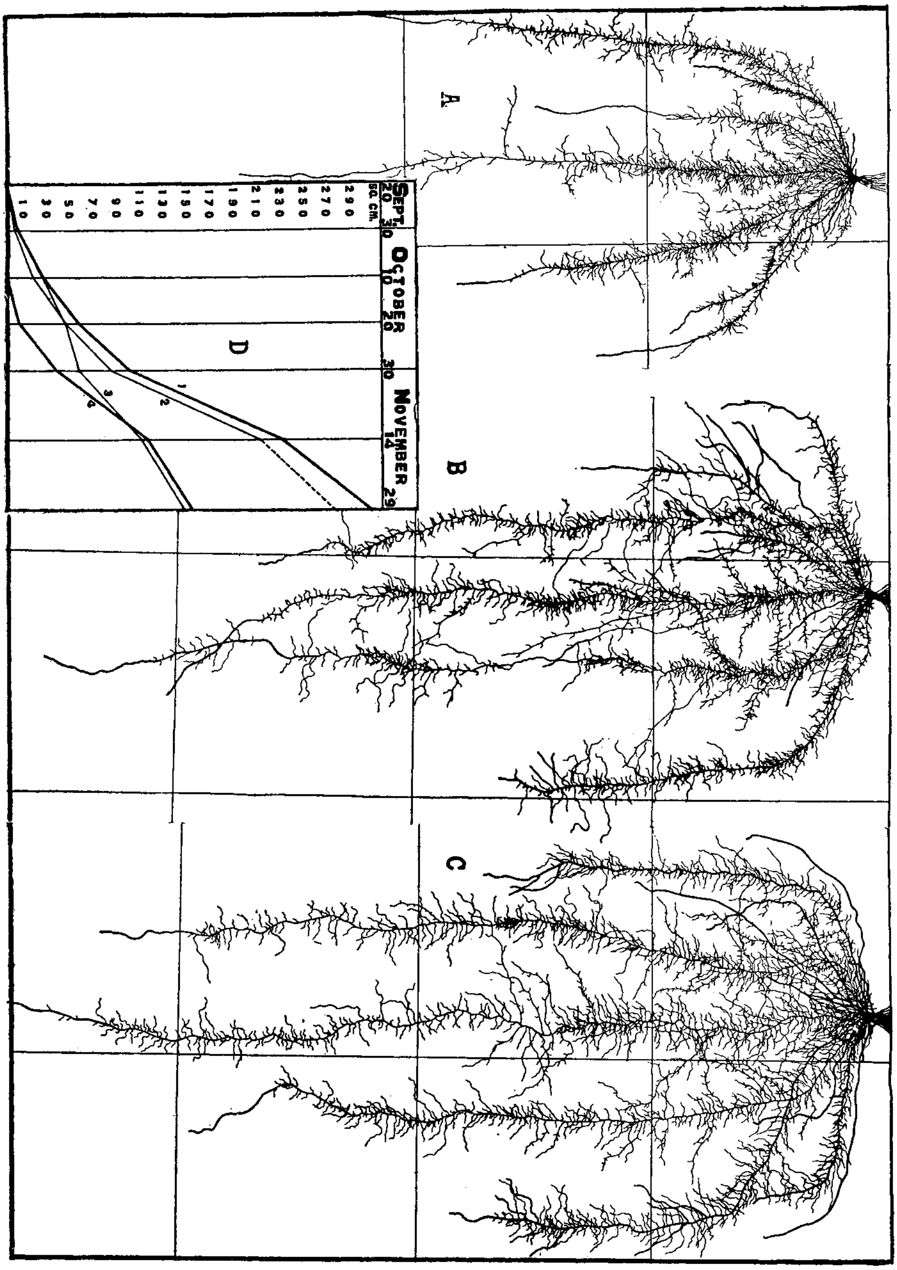

FIG. 4. A. Root habit of 40-day-old plant of winter wheat.

B. Roots of 55-day-old plant.

C. Root system on November 29. Winter wheat 70 days old. Squares represent square feet. All root systems drawn to scale.

D. Graphs showing: 1, the absorbing area (exclusive of root hairs); 2, the photosynthetic and transpiring area; 3, the absorbing area of the primary root system; 4, the absorbing area of the secondary root system.

devoid of branches. All of the main roots were so densely clothed with root hairs, to which the soil clung tenaceously, that the 0.5 to 2 inches of smooth, glistening white tips stood out in marked contrast.

Growth conditions during this interval in 1922 were very similar to those of 1921. Owing to some slight damage to the tops of the plants by grasshoppers the average photosynthetic area of 15 plants was used rather than that of the particular plants selected for the root area measurements. Although the photosynthetic area had increased from 50 to 89 sq. cm., during the 10 days the roots had grown equally well (from 61 to 105 sq. cm.) and their area still exceeded that of the green tops. The secondary system furnished 40 per cent of the absorbing area, but, owing to the greater thickness of these roots and the lesser degree of branching, only 25 per cent of the length, which was now 840 cm.

Fifth Period, October 30 to November 14

Although the temperature decreased rapidly during this period (ave. day 47° F., night 37° F., soil at 3 inches 45° F., see fig. 5), still the crop made an excellent growth. The weather was prevailingly clear and dry. The day and night humidities were 57 and 83 per cent respectively. The available water-content of the surface foot of soil averaged 10 per cent, that of the second foot about 7 per cent. The crop maintained a good green color. Although the drill rows were 8 inches apart, over much of the field the soil was practically concealed by the plants, which had a radial spread of about 4.5 inches. The average height was only 3 inches, owing to strong recurving of the short stems which gave the plants a prostrate habit. Tillering had increased rapidly from 7 per plant 15 days earlier to 11, although some of the largest plants had 50 tillers (Table II). The steadily increasing number of tillers together with the leaf development of each tiller is shown in Table IV.

Table II. *Growth of wheat from September 20, 1921, to March 29, 1922*

Date	No. Lvs.	No. Tillers	Photo-synthetic Area	Dry Weight	Working Depth Primary Root System	No. Roots, Secondary System	Average Length of Secondary Roots
			sq. cm.	grams	inches		inches
Sept. 30	1.5	0.0	8.28	0.013	6.0	0.0	0.0
Oct. 10	3.5	1.6	21.50	0.046	11.0	0.8	0.7
Oct. 20	13.0	4.4	59.46	0.146	16.0	3.9	1.8
Oct. 30	20.6	7.2	93.98	0.239	20.0	8.7	2.1
Nov. 14	31.5	10.5	226.39	0.621	30.0	10.0	4.7
Nov. 29	39.7	13.8	——	0.835	36.0	11.0	5.4
Dec. 14	42.5	15.1	——	0.882	36.0	11.0	7.0
Jan. 13	40.0	——	——	0.697	——	——	——
Feb. 12	40.5	14.8	——	0.556	——	——	——
Mar. 14	45.0	15.3	——	0.490	——	——	——
Mar. 29	61.0	17.7	——	0.727	36.0	——	——

On an average each plant now had 32 leaves, 18 of which were fully grown. This was an increase of 11 over that of October 30. The photosynthetic area (now 226.39 sq. cm.) had increased 141 per cent during the 15-day period (Table II). The dry weight of tops had increased 160 per cent, now being 0.621 grams.

Many of the roots of the primary system had reached a depth of over 3 feet, the thick, white, turgid root ends being quite abundant at this level, while a few were found at a depth of 4 feet. The branching habit of the primary root system had evidently changed but little in the surface 2 feet of soil except that the branches had somewhat elongated. The younger portions, as the roots deepened, became clothed with laterals similar in number and in secondary branching to that already described for the second and third foot of soil.

Each plant now had an average of 10 secondary roots (fig. 4B). They varied in length from .1 to 22 inches, with a working level of about 7 to 9 inches, a maximum lateral spread of 10 inches, while some reached a depth of 20 inches. They ran out almost horizontally or obliqued downward so slightly that few or none occupied the area under the plant where the primary roots were absorbing.

All of these thick, white roots were densely clothed with root hairs except on their rapidly growing ends. The branching was various. About half of these roots were unbranched or nearly so. Others were profusely branched throughout at the rate of 8 or more laterals per inch. These branchlets averaged about an inch in length, although some exceeded 5 inches. Only a few secondary branches occurred on these rootlets. In some cases the bulk of the branching occurred within a distance of 3 or 4 inches from the place of origin of the main root, while in others it extended to near the root ends.

Climatic conditions during this period in 1922 were not strikingly different from 1921 except for a few days of heavy rains, which, of course, affected only slightly the water-content of the nearly closed containers. However, some differences, due probably to a more uniformly moist soil in the containers, were noted at this excavation. The branches on the primary roots in the first two feet of soil were longer, as were also those on the secondary root system. Some of the latter reached 9 inches. Moreover, the length of the roots of the secondary system was slightly greater; otherwise the root habit was like that of the preceding season. The total root area, all of which was apparently actively absorbing, and except for the tips, covered with functional root hairs, was 237.5 sq. cm. This was an increase of 126 per cent during the 15-day interval. The area of the secondary root system now exceeded that of the primary by about 5 per cent. The former had made an increase in area of 187 per cent during the period, while the primary root system had increased only 84 per cent. Owing to the relatively finer roots of the primary system coupled with more profound branching, its total length, 15.1 m., still greatly exceeded that of the secondary system, 11.7 m. (Table

III). The photosynthetic area (215.3) was, as before, somewhat less than the absorbing area of the roots, exclusive of root hairs.

TABLE III. *Length and absorbing area of root system (exclusive of root hairs) and photosynthetic area of tops, 1922*

Date	Area Primary Root System	Area Secondary Root System	Total Area of Root System	Photo-synthetic Area of Tops	Length of Primary Root System	Length of Secondary Root System	Total Length of Roots
	sq. cm.	sq. cm.	sq. cm.	sq. cm.	cm.	cm.	cm.
Sept. 30.........	9.63	0.00	9.63	7.68	95.05	0.00	95.05
Oct. 10.........	31.02	0.37	31.39	22.50	323.87	1.50	325.37
Oct. 20.........	50.31	11.20	61.51	50.50	490.40	40.70	531.10
Oct. 30.........	62.80	42.32	105.12	88.98	632.70	207.45	840.15
Nov. 14.........	115.97	121.54	237.51	215.30	1,509.70	1,171.80	2,681.50
Nov. 29.........	151.76	157.92	309.68	280.00	2,004.70	1,234.70	3,239.40

SIXTH PERIOD, NOVEMBER 14 TO 29

Temperature conditions during this period were unfavorable for growth. During 5 consecutive days the average day and night temperatures remained below freezing—*i.e.*, 26° and 19° F. respectively. Temperatures of 10° F.

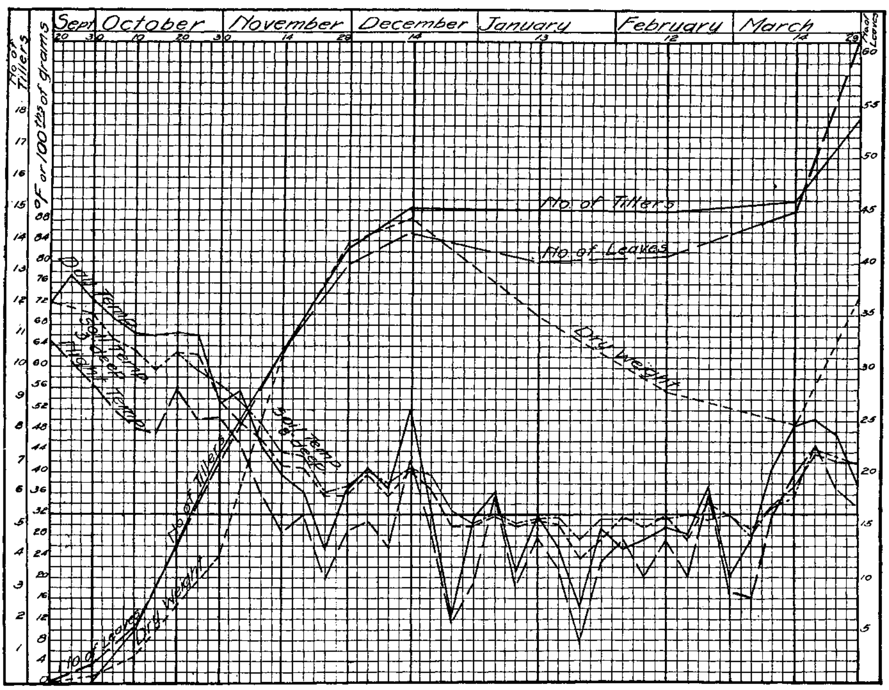

FIG. 5. Graphs showing the growth rate of winter wheat, and the temperatures of soil and air. The heavy horizontal line is 32° F.

for 10 consecutive hours were recorded, while the average daily temperature for the whole period was only 30° F. (fig. 5). The soil temperature at three inches depth remained 4° to 9° F. above freezing, although the surface soil was frozen solidly in places to 2.5 inches for two or three days. Water-content above the hygroscopic coefficient ranged from 7 to 12 per cent. Most of the days were cloudy and the humidity was relatively high (66 per cent by day). Although some of the tips, mostly of the older leaves, were frozen, the crop looked very well, a yellowish tinge being imparted by the normally deteriorating oldest leaves. The height and spread of the plants had not changed measurably. The stems, which were one or two inches long, were more conspicuous than before and on both parent plants and tillers curved back strongly. Notwithstanding the prevailingly low temperatures the crop made a good growth. The number of tillers per plant had increased from 11 on November 14, to 14. The rapidity of the appearance of new tillers and the rate of development of the older ones is shown in Table IV. Since some leaves had completely deteriorated and others had been frozen the photosynthetic area was not determined. The dry weight of tops had increased 34 per cent and was now 0.835 g.

TABLE IV. *Average number and development of tillers*

<table>
<tr><th>Date</th><th>With One Leaf</th><th>With Two Leaves</th><th>With Three Leaves</th><th>With Four Leaves</th><th>With Five or More Leaves</th><th>Total Number Tillers</th></tr>
<tr><td></td><td>per cent</td><td>per cent</td><td>per cent</td><td>per cent</td><td>per cent</td><td></td></tr>
<tr><td>Oct. 10</td><td>63</td><td>37</td><td>—</td><td>—</td><td>—</td><td>1.6</td></tr>
<tr><td>Oct. 20</td><td>48</td><td>29</td><td>23</td><td>—</td><td>—</td><td>4.4</td></tr>
<tr><td>Oct. 30</td><td>44</td><td>28</td><td>28</td><td>—</td><td>—</td><td>7.2</td></tr>
<tr><td>Nov. 14</td><td>30</td><td>20</td><td>28</td><td>20</td><td>2</td><td>10.5</td></tr>
<tr><td>Nov. 29</td><td>31</td><td>25</td><td>15</td><td>16</td><td>13</td><td>13.7</td></tr>
<tr><td>Dec. 14</td><td>33</td><td>23</td><td>20</td><td>11</td><td>13</td><td>15.1</td></tr>
<tr><td>Mar. 14</td><td>22</td><td>27</td><td>24</td><td colspan="2">27</td><td>15.3</td></tr>
<tr><td>Mar. 29</td><td>4</td><td>22</td><td>34</td><td colspan="2">40</td><td>17.7</td></tr>
</table>

An examination of the primary root system showed that a few roots had reached a depth of 4 feet, while the soil was well occupied to a depth of 3 feet. Thus some growth in depth had occurred since November 14, while branching had considerably increased. Only the stele of these roots remained intact in the surface 12 to 14 inches. Judging from the 1922 results this early deterioration, which was first noticed on October 30, must have been due to the rather low water-content of the surface soil, and especially a drier layer at about 8 to 20 inches.

The number of roots of the secondary system had increased from 10 (November 14) to 11, and in average length from 4.7 inches to 5.4 inches. Moreover, on November 14, 57 per cent of these were 2 inches or less in length, while at this examination only 8 per cent fell in this group of short roots. The percentages of roots less than 4 inches in length were 72 and 27 on November 14 and 29 respectively. This indicates clearly that the chief development had been not in the formation of new roots but the elongation of those already formed. Some reached a maximum depth of 22 inches (fig. 4C). Owing to the fine structural condition of the soil practically all of these could be removed in their entirety by working from below upward. The bright white root ends were very conspicuous and could easily be recovered in case of breakage, which was rare. Branching had increased considerably. Although some roots still had relatively few or no branches, especially those less than 150 mm. long, most of them were branched at the rate of 12 to 17 laterals per inch. These varied in length from a few mm. to 4 inches. Secondary laterals were sparce, few reaching a length of over 10 mm.

During 1922 weather conditions were more favorable for growth. However, deterioration of the older leaves made it difficult to determine accurately the photosynthetic area. It had increased to approximately 280 sq. cm. The dry weight of the plants was 0.855 grams, which was slightly in excess of that of the preceding year. The root development was very similar to that of 1921, except the roots of the secondary system were a little longer and the length of the branches was somewhat greater. The total area of the root system had reached 310 sq. cm., which was an increase of 30 per cent over the previous determination 15 days earlier. The secondary root system, as before, furnished slightly more than half of the absorbing area, its increase in growth rate approximately paralleling that of the primary system (fig. 4C). Although the soil had a good water-content at this time, deterioration of the cortex of the main roots of the primary system was well advanced. On November 14 it was just beginning, but at this time the cortex on about the first 10 inches of these roots was either destitute of root hairs or sloughed off, leaving only the stele intact. This is apparently a normal process, but occurred a little later than in 1921. However, this reduced the absorbing root area, as indicated by the presence of turgid root hairs, by only one third of one per cent.

Seventh Period, November 29 to December 14

Higher temperatures accompanying sunny weather and relatively low humidity (57 per cent by day) characterized this 15-day period. Like the two preceding periods, no precipitation of sufficient amount to affect the water-content of the soil occurred, and drought was accentuated. Only about 7 per cent available moisture was present to a depth of 4 feet. Yellowing of the older leaves was progressive, and blackened tips of frozen ones were somewhat in evidence. Thus far the season had been remarkably free from wind, but during a part of this period considerable blowing of the dry surface soil occurred.

Compared with preceding periods, the growth of the crop was small. Tillers had increased only about one per plant and the total number of leaves from 40 to 43. Moreover, little growth was determined in the number of leaves per tiller. A gain of only 6 per cent in dry weight (now 0.882 gram) had been attained. The curves of growth (fig. 5) show clearly that the maximum development for the season had been attained at this time.

The primary root system had practically ceased growing by November 29, at least the most careful examination showed no differences from the conditions obtaining on that date, except that the cortex on the main roots had shriveled to a depth of about 16 inches.

The usual count on 30 selected plants showed that the roots of the secondary system had not increased in number. Moreover, the working level had not deepened. The chief difference was an increase in length of the roots already formed. On November 29 these had an average length of 5.4 inches, but at this examination had increased to 7 inches. The manner in which these roots obliqued outward and formed an absorbing network in the shallower soil is worthy of notice. For example, it was not unusual to find roots spreading laterally 8 or 9 inches from the parent plant and ending at a depth of only 6 inches. The number and length of branches had increased proportionally with root elongation. Plants arising from seed which was deeply sown had a more poorly developed root system.

In 1922, cold weather, which checked the growth of the crop, began early in December, and it is probable that the absorbing area of the roots was only slightly increased until growth was resumed in the spring.

Eighth Period, December 14 to January 13

Conditions for growth either above or below ground did not prevail during this period. Zero weather on December 22, with an average temperature of only 4° F. for 48 consecutive hours, was followed by a light snow which covered the ground for three days. The soil, which had a water-content ranging from 4 to 10 per cent in excess of the hygroscopic coefficient, was frozen during most of the time to a depth of 2 to 7 inches, while surface thawing occurred repeatedly. The average day humidity was 71 per cent. A second light snow, accompanied by zero weather, occurred on January 4 and cold weather prevailed during the remainder of the period.

Damaging effects of winter conditions were shown both by the freezing and mechanical injury to leaves. Frozen areas were easily recognized because of their dark-blue, rather metallic color, their water-soaked appearance, and greater transparency in transmitted light. Mechanical injuries such as wind whipping of the leaves, frozen snow on the blades, freezing of the lower surfaces to the ground, etc., were pronounced. The extent of injuries which accounts for the decrease in dry weight from 0.882 to 0.697 gram are shown in Table V. Mature leaves, which were more exposed, suffered the greatest damage. Otherwise, with rare exceptions, only the long, narrow leaves developed from the youngest tillers were completely frozen. The number of tillers remained constant and few or none were entirely killed. A green carpet with streaks of brownish yellow, the deteriorated leaf tips between the drill rows, characterized the field.

TABLE V. *Deterioration of leaves of 50 plants selected on the several dates*

Date	Uninjured	Tips to One Third of Leaf Injured	One Half to Two Thirds of Leaf Injured	Entire Leaf Injured
	per cent	per cent	per cent	per cent
Jan. 13	21	52	23	4
Feb. 12	19	27	37	17
Mar. 14	32	10	26	32
Mar. 29	49	9	14	28

NINTH PERIOD, JANUARY 13 TO FEBRUARY 12

During the entire period the average day and night temperatures were below freezing, the weather being more severe than during the preceding interval. A minimum of —7° F. occurred, and for 16 consecutive hours the average temperature was —3° F. During the entire period the soil was frozen to depths varying from 4 to 12 inches, except for three or four surface thaws. The water-content above the hygroscopic coefficient ranged from 5 to 19 per cent. The temperature at 3 inches depth averaged constantly below freezing and at times was as low as 17° F.; at 8 inches depth it was below freezing during much of the period; but at 15 inches 34° F. was the lowest temperature recorded. Light snows covered the crop for periods of two or three days at two different times, while on another date a light sleet occurred. Temperature changes from 20° F. to 40° F. from morning to noon were not infrequent.

These environmental conditions caused increased injury to the crop, the dry weight showing a decline of 20 per cent over that of January 13, and a total loss of 37 per cent since the cessation of growth on December 14. The position of certain leaves was carefully marked and a study made of the causes of their deterioration. In most cases injury or death resulted from freezing and thawing, freezing to the soil, or wind whipping when the leaves were frozen or jacketed with ice. Often local injuries occurring at the base of the leaf resulted in total death. Usually death of the leaf resulted only after repeated freezing and thawing. The condition of the leaves on February 12 is shown in Table V.

Superficially the crop at this time looked brownish and almost dead, but closer examination revealed the healthy condition of the culms and the younger leaves. The usual counts on 50 selected plants showed that the number of tillers remained practically the same as before.

Table VI. *Average air and soil temperatures in degrees Fahrenheit, and relative humidity in per cent from September 20, 1921, to March 30, 1922*

Date	Air Temperatures		Soil Temperatures			Relative Humidity	
	Day	Night	Depth 3 In.	Depth 8 In.	Depth 15 In.	Day	Night
Sept. 20–25	77.2	61.2	71.7	71.7		41.1	77.1
Sept. 25–30	72.9	56.6	69.9	69.0		39.9	70.7
Sept. 30–Oct. 5	69.0	51.8	65.6	64.0		34.9	62.4
Oct. 5–10	66.2	48.6	63.3	63.5		34.3	67.8
Oct. 10–15	66.0	47.1	59.4	60.0		34.0	55.6
Oct. 15–20	66.1	55.5	62.6	62.0		39.1	64.6
Oct. 20–25	66.0	50.0	62.5	58.8		42.0	64.0
Oct. 25–30	52.7	50.3	53.7	56.6		70.5	75.5
Oct. 30–Nov. 4	55.5	45.3	49.3	53.5		49.6	77.4
Nov. 4–9	45.1	35.8	46.0	49.0		66.1	89.5
Nov. 9–14	39.1	28.3	41.0	43.6		54.2	83.0
Nov. 14–19	35.9	32.0	40.8	43.0		73.5	84.5
Nov. 19–24	25.6	19.3	35.5	36.0		60.6	77.1
Nov. 24–29	36.1	28.2	35.5	37.0		64.3	86.2
Nov. 29–Dec. 4	40.5	30.5	39.6	39.2		61.5	83.3
Dec. 4–9	36.7	25.8	35.7	37.6	41.5	58.5	81.1
Dec. 9–14	51.6	42.0	40.0	40.5	42.6	49.5	73.0
Dec. 14–19	33.0	28.3	36.8	39.5	42.8	65.5	75.7
Dec. 19–24	12.3	11.0	29.6	32.5	39.2	79.0	85.3
Dec. 24–29	31.2	18.3	29.6	30.0	37.5	70.1	88.1
Dec. 29–Jan. 3	36.0	35.0	31.6	31.6	37.5	57.0	79.6
Jan. 3–8	21.0	18.0	29.5	30.2	36.5	79.0	91.4
Jan. 8–13	32.0	27.4	30.9	30.8	36.0	74.6	84.1
Jan. 13–18	25.4	21.7	30.0	30.8	35.5	78.2	77.3
Jan. 18–23	14.4	7.8	23.7	27.0	34.2	69.4	66.2
Jan. 23–28	29.3	22.4	27.0	31.0	34.2	75.0	84.7
Jan. 28–Feb. 2	25.4	27.1	31.6	31.0	34.2	74.5	80.7
Feb. 2–7	26.5	20.0	29.5	31.0	35.0	50.0	73.3
Feb. 7–12	29.4	27.0	31.6	31.0	35.0	55.1	64.5
Feb. 12–17	28.0	20.0	27.0	32.0	35.0	42.5	61.2
Feb. 17–22	37.0	35.2	34.0	31.0	34.0	70.2	72.2
Feb. 22–27	20.0	17.2	31.8	32.0	35.0	65.0	73.7
Feb. 27–Mar. 4	27.2	16.0	29.0	28.0	34.0	50.4	70.0
Mar. 4–9	40.3	31.6	33.5	33.0	34.0	61.9	79.0
Mar. 9–14	48.6	39.2	37.0	35.0	35.0	58.0	84.0
Mar. 14–19	50.0	45.0	43.5	44.5	38.0	72.6	89.0
Mar. 19–24	47.0	37.0	42.0	43.0	41.5	68.0	84.1
Mar. 24–29	37.0	33.8	41.7	42.0	41.5	74.0	86.2

Tenth Period, February 12 to March 14

During this period the days were longer, less cloudiness prevailed, and temperatures were somewhat higher. The ground was covered with snow during two days only. Repeated freezing and thawing of the surface soil resulted in slight damage by heaving. Water-content of the surface foot of soil above the hygroscopic coefficient was about 15 per cent; the deeper soil was drier (5 to 9 per cent). During much of the period the soil was frozen to 8 or 12 inches, and during days of warm winds and low humidity deterioration of the leaves probably resulted in part from drought. By the end of this interval 32 per cent of the leaves were entirely killed, but owing to the appearance of new ones, the per cent of uninjured leaves had increased to 32. Following February 20, when certain young leaves were marked to determine their activities, it was found that growth was proceeding slowly at an average temperature of 35° F., the days being bright and clear. Many leaves elongated 1 to 3 mm. during a 30-hour period. Growth was checked until March by a recurrence of freezing weather. During the second week in March frost entirely disappeared from the soil, and the temperatures rapidly increased. The weather was clear and the crop began to take on renewed growth. However, this was not sufficient to counterbalance the loss in weight due to winter deterioration, a total loss of 12 per cent over that of February 12 being determined. Both tillers and number of leaves increased slightly over that of the preceding period.

Eleventh Period, March 14 to 29

During this interval environmental conditions were much more favorable, and the crop responded by making a vigorous growth. Frost had entirely disappeared from the soil which was rapidly warming up (Table VI). Water-content above the hygroscopic coefficient varied from 7 to 20 per cent, being highest in the surface soil where recent rains had replenished the supply. The average day and night temperatures ranged between 34° and 50° F. The days were longer and clear weather prevailed. By the end of the period, notwithstanding the advent of some snow and cold rains accompanied by freezing temperatures, the field assumed a new aspect, the brownish appearance being replaced by one of green as the dead leaves were hidden by the new foliage. Less of the bare soil was exposed.

The number of tillers had increased from 15 (December 14) to 18. Only a few tiller buds remained, indicating that the maximum tiller production had approximately been attained. The leaves had likewise increased in number from 42 to 61, a gain of 45 per cent. The culms began to grow erect and the spikes in the largest tillers were a millimeter in length. The dry weight had increased to 0.727 g., a gain of 48 per cent over that 15 days earlier. Thus the initiation of a new period of growth was unmistakable.

A final examination of the roots was made at this time. The primary root system was apparently in a condition similar to that of December 14, when cold weather began. No increase in depth or branching was apparent. However, the roots below 18 inches appeared to be in as good condition as at the last examination on December 14. Some of the roots of the secondary system had begun renewed growth. Moreover, many new roots, now only 3 to 10 mm. long, had originated from the tillers, especially near the center of the crown. Thus, just as in early winter cessation of root growth corresponded in general with that of tops, so its resumption occurred at about the same time. Although root development was not followed further, it is of interest to note that the mature root system of winter wheat grown in similar soil at Lincoln reached depths of 5 to 7 feet.

Discussion

A survey of these data shows that the development of the crop fell into three rather distinct periods, temperature being the controlling factor. The first period with a duration of 85 days, September 20 to December 14, was one of vigorous vegetative development; the second of 90 days' duration, extending to the second week in March, was one of apparent dormancy; while the third began with a slow renewal of growth which became rapidly accelerated with rising temperatures.

The very favorable soil moisture conditions, and especially the high temperatures under which the seeds germinated readily, accounts for the vigorous growth and abundant tillering of the plants (*cf.* Walster, 1920). Tiller production started 15 days after planting and was kept up continuously until the middle of December, even after the advent of temperatures which averaged below freezing for 5 consecutive days. Leaf output paralleled the growth of tillers. Because of the abundant leaves and tillers, all growing from a single narrow base, and the consequent spreading or pushing apart of the older leaves, normal deterioration of the latter started early and continued throughout the season. Due to the crowding of the tillers the plants assumed a rosette-like position, which undoubtedly eliminated excessive transpiration and modified soil temperatures (*cf.* Bouyoucos, 1916; Salmon, 1917). The water-content of the soil became rather low, especially in the deeper layers, after October 10, the precipitation being less than normal for this season. However, the bright autumn days were conducive to growth, temperature being the controlling factor. The greatest increase in both tillers and leaves occurred between October 10 and 20 (175 and 271 per cent respectively) at an average daily temperature of 59° F. No marked change, however, in the upward direction of the graphs representing these indices of growth occurred even during late November when some of the leaf tips were frozen and night temperatures continuously averaged below freezing while those of the day were only 33° F. The soil temperature, however, was several degrees above freezing. As a result of these low temperatures, which continued through the first 10 days of December, growth was perceptibly checked and the gains made were much less than during any preceding period. While a dry layer of soil at 8 to 18 inches in depth, coupled with warm days and occasional dry winds, may have had some effect in decreasing the growth rate, it was more probably due, for the most part, to physiologically retarding influences brought about as a result of repeated freezing. The slowing down in rate of growth probably was accompanied by a "hardening" process, the chief feature of which is the retention of water by the protoplasm. Rosa (1921) states that "any treatment materially checking the growth of plants increases cold-resistance. In many plants hardiness increases in proportion as growth is checked." He finds that a decreased water-content and an increased water-retaining power accompany a condition of greater cold resistance in plants. It is of interest to note that growth progressed rapidly as measured by leaf and tiller production from November 14 to 29, when the average daily temperature of 30° F. (33° F. day, 27° F. night) was far below the generally accepted physiological minimum of 40° F. (*cf.* Livingston, 1916). The graph indicating growth based on dry weight, in general, parallels those of tiller and leaf production. Deviations in the graph during November are probably due to the increased size of the base of the stems. All reached a maximum on December 14. The photosynthetic area closely approximated that of leaf production.

The primary root system developed with marked rapidity; the general working level increased quite uniformly at the average rate of 0.55 inches per day during the first 55 days and reached the three-foot level before the period of dormancy began. Extent of branching correlated with growth in length. The development of a secondary root system began, as in native grasses (Clements and Weaver, 1922), synchronously with the appearance of tillers. Its most rapid development, whether measured by the number of roots or their average length, occurred, as did that of tiller and leaf production, during the third ten-day period after planting. On an average a new root and a new tiller developed every 4 or 5 days until the middle of November, after which the rate of tillering exceeded that of root production. However, the increase in average length of the roots of the secondary system continued synchronously with tiller production and at an undiminished rate until the middle of December. Moreover, branches on the roots already produced continuously increased in extent, thus keeping a balance between absorption and transpiration. These roots increased in average length only about 0.1 inch per day, the average being kept low by the constant appearance of new roots. Actually the growth of the individuals often proceeded at the rate of 0.4 or 0.5 inch per day, some reaching a depth of 22 inches before the cessation of growth in the middle of December.

Root areas in 1922, during which growth as measured by photosynthetic area was very similar to that of 1921, increased progressively with that of tops and was uniformly 10 to 35 per cent greater in extent. Since microscopic examination indicated that all of the roots and their branches were clothed with functioning root hairs, except at the growing tips, the absorbing area was probably eight or ten times greater than the transpiring area (*cf.* Schwarz, 1883). The primary root system increased its absorbing area from 10 to 63 sq. cm. during October, and to 152 sq. cm. during November, the greatest percentage of increase occurring, as did that of tops, during the second 10-day period of growth. The secondary root system also made its greatest growth as regards absorbing area during the first 25 days after the appearance of these roots. On October 10 it made up only 1 per cent of the absorbing area, but this was increased to 18 and 40 per cent in the two following 10-day intervals respectively, while by November 14 it furnished 51 per cent of the total absorbing area.

The total length of all the roots reached 27 meters at the age of 55 days. Upon the advent of dormancy (December 14) the length had increased to 32.4 meters. The secondary root system, owing to the greater thickness of the main roots, made up only 38 per cent of the total root length.

The second period, one of dormancy, was initiated about the middle of December and continued with slight interruption until the second week in March. Throughout almost the entire period the day and night temperatures averaged below freezing and at certain times fell to 8° to 12° F. The soil was frozen to a depth of 6 to 12 inches except for an occasional thawing of the surface. Little precipitation occurred, and the crop was covered with snow for only a few days.

Growth was ended abruptly at the beginning of this period by zero weather, with an average temperature of only 4° F. for 48 consecutive hours. There was no increase in tiller production; repeated counts showed that the number remained practically constant. The number of leaves, and consequently the dry weight of the plants, decreased as a result of the unfavorable conditions. Some injury occurred from desiccation, but the chief causes were repeated freezing and thawing and mechanical injury such as wind whipping of the leaves, frozen snow on the blades, and freezing to the ground. Deterioration of the leaves was most pronounced among those that were fully grown. Large numbers of small, partly developed leaves remained uninjured. Eckerson (1917) has shown that "throughout the growth of the wheat plant the young parenchyma cells (the meristem) of any growing region contain a greater amount of fructose and of asparagin than the adjacent parenchyma cells." Macfarlane (1913) observed that all thermo-resistant plant structures have a rich and relatively dense protoplasm or a stored mass of reserve material in the cells that contributes to their thermo-resistant qualities. Rosa (1921) found that the increased water-retaining power of the hardened tissue is associated with decreased moisture content, increased amount of hydrophilous colloids such as pentosans, increased water-retaining power of such cell colloids because of a slight increase in acidity or other internal changes, as well as an increased amount of osmotically active substances such as soluble sugars. The first three factors may become operative in a very short period of time, when the activity of the plant is limited by any factor; the last is probably important only in plants hardened by prolonged exposure to cold. The older leaves of wheat not only have larger vacuolated cells and more "free" water, but they are also more exposed on account of their size and position to the factors causing deterioration.

Damage of leaves was progressive. On January 13 only 4 per cent were totally injured, but this had increased to 32 per cent by March 14. Conversely the leaves which escaped injury during the early winter apparently had an increased resistance, so that the number of uninjured leaves remained almost constant (20 per cent) until growth was renewed. However, the leaves which were only slightly damaged on January 13 (52 per cent) fell to 27 per cent by February 12. Anthocyanin occurred in abundance especially in the injured leaves, its formation probably being directly connected with a disturbance of the photosynthetic activity (*cf.* Wheldale, 1916). The small amount of injury due to desiccation on clear, relatively warm, windy, winter days may be due in part to the water supply furnished by the portion of the primary root system below the frozen soil layer, although undoubtedly some water was absorbed in the surface foot where the temperature (at 8 inches depth) fluctuated within the limits of 30° to 31° F. Even at 3 inches depth it averaged only a few degrees below freezing and only once fell to 17° F. for about 20 hours. Bouyoucos (1920) has shown that the temperature may fall to 25° F. and still not all of the soil water will crystallize out. The importance of snow in protecting vegetation against freezing has apparently been greatly overestimated (*cf.* Smith, 1919; Root, 1919; Meisinger, 1920). The decrease in dry weights of tops was 21 per cent by January 13, and 37 per cent by February 12, while on March 14, notwithstanding some renewed growth, it was 44 per cent less than on December 14.

The root system, even that part subjected to the greatest temperature changes, was apparently uninjured. A layer of soil at least an inch or two thick above the zone of root growth acted as an efficient protection. Temperatures not only averaged much higher than those above ground, but the fluctuations were both much slower and of lesser degree; changes greater than 8° F. at a depth of 3 inches in a 24-hour period were rare. Throughout the period the soil was fairly dry. McCool and Millar (1917) have shown that as the soil moisture decreases the freezing point of the root cell sap is lowered.

On February 20 some growth of the leaves occurred at an average daily temperature of 35° F. It is possible that slight growth may have taken place during a similarly warm period in January, but this was not ascertained. However, both of these periods were of brief duration.

The initiation of a new period of practically uninterrupted growth took place during the second week in March. Frost disappeared from the soil as the air temperature became higher, and the crop developed slowly at a daily average of less than 40° F. Rains replenished the water-content especially in the surface soil and with increasing temperatures the crop made a steady growth. The root system came through the winter quite uninjured, and began renewed growth synchronously with the tops. The primary root system was apparently functioning as in late fall. During two weeks with an average temperature of 42° F. the plants increased their tillers from 15 to 18 in number, while the number of leaves increased 36 per cent. Many new roots of the secondary system also appeared. The culms began to grow erect and the spikes to develop. The crop assumed a new aspect as the dead brown leaves were hidden by the green of the new foliage.

The vigorous growth in early spring, due to the well-developed root system and culms stored with food, permitted the rapid replacement of the deteriorated photosynthetic system. Thus in a period of two weeks, during a part of which it was cloudy and rainy with freezing weather accompanied by snow, the crop had regained 60 per cent of the loss in dry weight that occurred during the winter.

Summary

Kanred winter wheat was grown at Lincoln, Nebraska, under field conditions during 1921 and 1922. Growth rate as indicated by dry weight of tops, photosynthetic area, number of leaves and tillers, number, length, and absorbing area of roots was determined at ten-day intervals during the fall and at longer intervals during winter and spring. Favorable environmental conditions promoted rapid development. Tiller production started 15 days after planting and a new tiller was added every 4 or 5 days until December, when an average of 15 tillers and 43 leaves per plant was attained. The photosynthetic area increased to 226 sq. cm. by the middle of November and closely paralleled the increase in dry weight, which reached its maximum (0.882 gram) by December 14. Growth progressed rapidly, in late November, at average daily temperatures of 34° F.

The roots consisted of a primary system of 3 roots which penetrated rather vertically downward, at the rate of over half an inch a day, and, branching widely, reached depths of 3 or 4 feet by the middle of December. Development of the secondary root system was correlated with that of tiller production, a new root being added every 4 or 5 days until the middle of November, after which the chief growth was not in number, but in elongation and branching. By December the secondary root system consisted of 11 roots, some of which were 22 inches deep. They constituted half of the total absorbing area, which was 310 sq. cm., and 38 per cent of the total root length, which was 32.4 m. Root growth ceased simultaneously with that of aboveground parts.

During the 90 days of dormancy the dry weight of tops, due to leaf deterioration, decreased 44 per cent. Progressive deterioration of the older leaves occurred, but leaves that escaped injury early in the winter deteriorated little, 20 per cent remaining undamaged. The roots were apparently uninjured, although the soil was frozen at times to a depth of 12 inches.

Leaf growth took place slowly in February at an average daily temperature of 35° F. During the last half of March both roots and shoots resumed growth, and in less than two weeks at an average temperature of 42° F. the crop regained 60 per cent of the loss in dry weight which had occurred during the winter.

BIBLIOGRAPHY

Brenchley, W. E., and V. G. Jackson. 1921. Root development in barley and wheat under different conditions of growth. Ann. Bot. **35**: 533–556.

Bouyoucos, G. J. 1916. Soil temperature. Mich. Agr. Exp. Sta. Technical Bull. **26**: 1–133.

——. 1920. Degree of temperature to which soils can be cooled without freezing. Jour. Agr. Res. **20**: 267–269.

Chandler, B. B. 1914. The killing of plant tissue by low temperature. Mo. Agr. Exp. Sta. Res. Bull. **8**: 143–309.

Clements, F. E., and J. E. Weaver. 1922. Transplant quadrats and areas. Yearbook Carnegie Institution of Washington, No. 21.

Eckerson, S. H. 1917. Microchemical studies in the progressive development of the wheat plant. Wash. Agr. Exp. Sta. Bull. **139**: 1–20.

Jackson, V. G. 1922. Anatomical structure of the roots of barley. Ann. Bot. **36**: 21–39.

Livingston, B. E. 1916. Physiological temperature indices for the study of plant growth in relation to climatic conditions. Physiol. Res. **1**: 399–420.

Macfarlane, J. M. 1913. The relation of plant protoplasm to its environment. Abs. in Exp. Sta. Record **28**: 326–327.

McCool, M. M., and C. E. Millar. 1917. The water-content of the soil and the composition and concentration of the soil solution as indicated by the freezing-point lowerings of the roots and tops of plants. Soil Science **3**: 113–138.

Meisinger, C. LeRoy. 1920. The effect of snow upon the growth of winter wheat. Sci. n. s. **51**: 639–640.

Nobbe, F. 1869. Die Pflanzencultur im Wasser und ihre Bedeutung für die Landwirthschaft. Die landwirthschaftlichen Versuchs-Stationen **11**: 106–111.

Root, C. J. 1919. Relation of snowfall to the yield of winter wheat. Mo. Weather Rev. **47**: 700.

Rosa, J. T. 1921. Investigations on the hardening process in vegetable plants. Mo. Agr. Exp. Sta. Res. Bull. **48**: 1–97.

Salmon, S. C. 1917. The relation of winter temperature to the distribution of winter and spring grains in the United States. Journ. Am. Soc. Agron. **9**: 21–24.

——. 1917. Why cereals winterkill. Jour. Am. Soc. Agron. **9**: 353–380.

Schwarz, F. 1883. Unters. aus d. bot. Inst. Tübingen, **1**: 135.

Smith, J. W. 1919. Effect of snow on winter wheat in Ohio. Mo. Weather Rev. **47**: 701–702.

Walster, H. L. 1920. Formative effect of high and low temperatures upon growth of barley: a chemical correlation. Bot. Gaz. **69**: 97–126.

Weaver, J. E.; Jean, F. C.; and Crist, J. W. 1922. Development and activities of roots of crop plants. Carnegie Inst. of Wash., Pub. No. 316.

Wheldale, M. 1916. The anthocyanin pigments of plants.