SEASONAL GROWTH OF GRASS ROOTS [1]

Irene H. Stuckey

In its broadest meaning, growth of a cellular tissue is an irreversible increase in size, in weight and in number of cells. To what extent any one of these phases alone may be considered growth depends entirely on the point of view. It is conceivable that one cell may divide and the total volume of the resulting two cells be no larger than the original single cell; however, that division occurred is evidence that the metabolic activity of the cell was greater than that existing during dormancy. Somewhat later in the development of the tissue, these two cells may elongate, thus increasing the size and possibly the weight of the tissue. This second phase may also be considered growth. In the subsequent discussion of root development, both cell division and root elongation are used singly as measures of growth, more for convenience than because of any attempt to differentiate among the several stages of growth.

Root growth and its influence on the subsequent development of the plant has always been recognized as important in respect to food and water relationships, and, although numerous observations of root development have emphasized the total amount and extent of roots, few investigators have studied the time of the year at which this growth occurs. Weaver (1926) and Weaver and Bruner (1927) described the growth of the roots of economic plants, but their studies were made almost entirely on soil types which do not occur along the Atlantic seaboard. As Sprague (1933) has pointed out, the study of roots under eastern conditions is necessary to utilize fully the soil resources there. Observations of the seasonal growth of roots over a period of a year or more have been published by a few investigators, McDougal (1916), Collison (1935), and Harris (1926), principally with fruit and forest trees. Worzella (1932) has compared root growth in hardy and nonhardy wheat in investigating winter killing of the latter. The development of the roots of several species of grass has been described by Sprague (1933) and Evans (1939). Sprague determined the weights of roots of colonial bent and Kentucky bluegrass produced during April, May, and June. Evans found a difference in root development of Chewings fescue, New Zealand browntop and fine-leaved sheep fescue under putting green conditions with different fertilizer treatments.

The purpose of this study was to determine at what time of the year new roots are produced on perennial grass plants and, if possible, how long they survive.

[1] Received for publication February 20, 1941.
Contribution No. 582 of the Rhode Island Agricultural Experiment Station. Acknowledgment is made to Dr. V. G. Sprague, Regional Pasture Laboratory, State College, Pennsylvania, for his generous assistance during the preparation of this manuscript.

Materials and methods.—Twelve species of grasses were used in the original experiment: timothy (*Phleum pratense* L.), Aberysthwyth pasture timothy S-50 (*Phleum pratense* L. var. S-50), Kentucky bluegrass (*Poa pratensis* L.), Canada bluegrass (*Poa compressa* L.), redtop (*Agrostis alba* L.), orchard grass (*Dactylis glomerata* L.), meadow fescue (*Festuca elatior* L.), perennial rye grass (*Lolium perenne* L.), Italian rye grass (*Lolium multiflorum* Lam.), rough-stalked meadow grass (*Poa trivialis* L.), crested wheat grass (*Agropyron cristatum* (L.) Beauv.). Only a few plants of Italian rye grass survived the first winter, and in October, 1939, this species was replaced by stolons of colonial bent (*Agrostis tenuis* Sibth.).

Grass seed of the species listed above was obtained from commercial seedhouses and planted in flats in September. As soon as the seedlings had reached a sufficient size, they were transplanted to a plot of well drained loam soil which had been divided into 36-inch squares with 12-inch boards sunk flush with the ground, three squares for each species. The partitions kept the roots of the species separated and facilitated digging the plants when the soil was frozen. A complete fertilizer and lime were added to the soil before the grass was planted but none thereafter.

The Canada bluegrass and timothy S-50 seeds germinated very slowly and the plants were smaller and transplanted later than the other species. However, they became established before winter began and suffered no ill effects. The growth of all plants seemed normal and compared favorably with the same species in other locations. The plants were cut only at the end of the summer when the dead seed stalks were removed.

For examination of the roots, several plants were dug with a large mass of soil enclosing the roots. If the adhering soil was dry much of it was shaken off and the plants washed on a screen. Five plants were usually used but when the soil was frozen, a chisel and sledge hammer were used to cut the blocks of soil and only one plant of each species was removed. The blocks of frozen soil containing the plants were immersed in buckets of cold water until thawed sufficiently for the plants to be removed. Then they were washed in the usual fashion and the root tips fixed in Craf solution, the whole process requiring no more than fifteen or twenty minutes.

The total mass and extent of the roots was noted only comparatively. Attention was focused on the actively growing roots, both those first emerging from the crowns and the mature roots which were producing new tips. These roots were examined macroscopically as to length, size, number, and appearance. During January, February and the first part of March, sections stained with Heidenhain's hematoxylin, or aceto-carmine smears were exam-

TABLE 1. *Dividing cells found in root tips.*

Species	Feb. 13, 1939	Mar. 3, 1939	Jan. 10, 1940	Jan. 29, 1940	Feb. 7, 1940	Mar. 13, 1940
Timothy	+[a]	+	+	+	+	+
Timothy S-50	+	+	+	+	+	+
Kentucky bluegrass	+	+	+	—	+	+
Canada bluegrass	—[b]	+	0	—	+	+
Redtop	+	—	—	—	+	—
Meadow fescue	+	—	0	—	+	+
Rough-stalked meadow grass	+	+	0	—	—	+
Orchard grass	0[c]	—	+	—	—	+
Crested wheat grass	0	+	+	—	—	+
Perennial ryegrass	0	—	—	—	—	—

The soil was frozen at the time the plants were dug. In some cases where no root tips were examined, all the tips were broken off, in others, no new roots were found.

[a] + Dividing cells found.
[b] — No root tips examined.
[c] 0 Dividing cells not found.

ined for evidences of mitosis. The presence or absence of dividing cells was the criterion of growth at this season. Metaphases were easier to recognize and were used as a standard, although other stages usually accompanied them.

Air temperatures were measured during the entire experiment by a thermograph in a case four feet above the ground. Soil temperatures were measured with soil thermometers from April 15 to December 26, 1939, but when one of the thermometers froze and broke, readings were discontinued. They were not satisfactory except during warm weather.

ROOT GROWTH.—The behavior of all species was very much alike during the first year. The seminal roots were active for six to eight weeks, gradually being replaced by adventitious roots from the crowns. New tillers developed very quickly after the seedlings became established, especially on those plats containing Kentucky bluegrass, Canada bluegrass and perennial ryegrass.

New roots emerged continually, and those which had developed earlier continued to grow well into December. The soil was frozen during January, 1939, and no roots were examined until February 13. At this time, dividing cells were found in some species, but not in others. These are shown in table 1. Mitotic figures were most numerous in the root tips of timothy, Kentucky bluegrass, and redtop. The soil had thawed by the first of March, and root growth was more active. The roots of rough-stalked meadow grass apparently did not begin to grow so early as some of the other species but in late March, forty to fifty new roots emerged almost simultaneously and elongated rapidly. In all the species, the development of new roots and elongation of existing roots was conspicuous in March and April, reaching its maximum during the first two weeks in April. After the blossom primordia made their appearance in May, few new roots were produced but growth continued at the tips of the roots which had developed earlier. Whether the production of new roots was terminated by unfavorable soil temperatures or inhibited by the developing flower primordia was not determined. In June, disintegration of the roots from the previous season was noted in all species to a certain extent but more pronounced in some than in others.

During the summer months, except for an occasional new tip on a mature root, no growth was noted. Neither elongation of existing roots nor development of new roots occurred to any great extent until the middle of October. At this time, differences were observed in the behavior of the species. In some species, numerous new roots emerged from the crowns and grew vigorously. By the time these roots had elongated to ten or twelve inches, many of the roots from the previous season had disintegrated. In other species only three to four new roots were produced on each plant, and as far as could be determined most of the roots which had developed during the previous season remained alive and functional. To date, no satisfactory test has been devised to determine whether mature grass roots are living or dead unless the roots are disintegrating. Kentucky bluegrass proved especially difficult. The roots were brown, wiry, and brittle and to all appearances dead in plants dug from several locations. The plants grew normally, however, and produced flowers and seeds. No quantity of new roots replaced these brown dry ones during the experiment.

Observations were continued through the winter of 1939–40. With the exception previously mentioned, that new roots were more numerous on some species than others, the behavior of the roots was very similar to that recorded during the winter of 1938–39. Root tips were collected January 10, January 29 (from the timothys only), February 7, and March 13. The absence of mitotic figures in some of these species was probably due to the small number of dividing cells present and the possibility of not finding them in the root tips examined rather than absence of cell divisions.

Whenever possible, ten root tips from each species were examined. At times, however, only one or two were obtainable.

Again, as in 1939, the elongation of the roots was extremely rapid after the soil had thawed in March. The maximum growth occurred during the first two weeks in April. The maximum production of new roots took place somewhat sooner, although it varied according to species. Root growth during the spring was very similar to that observed during the preceding fall. There were even more noticeable differences among species in the development of new roots. For the present the species studied are divided tentatively into two groups: one having "perennial" roots and the other "annual" roots, as is shown in table 2. If all the roots

Table 2. *Classification of root systems.*

"Annual"	"Perennial"
Timothy	Kentucky bluegrass
Timothy S-50	Canada bluegrass
Redtop	Orchard grass
Meadow fescue	Crested wheat grass
Rough-stalked meadow grass	
Perennial rye grass	
Colonial bent (probably)	

were regenerated each year, the old roots disintegrating shortly after the new ones became established, the root system was considered "annual." Whenever the maximum production of roots occurred during the first year and these roots, for the most part, remained functional for more than one year, the root system was designated "perennial." There was some growth during the second fall and spring and some disintegration of the first roots formed, but this amount of new growth and decay was small compared with the original root growth during the first fall and spring, and with the number of new roots produced by those species having "annual" roots. Most of these new roots developed from the nodes of the rhizomes, if rhizomes were present, or on the outermost edges of the crown of the plant.

Production of new roots ceased about the time that flower primordia were visible, although elongation at the tips of mature roots continued into June. By July, no further root growth was observed and the experiment was discontinued July 22, 1940. A summary of the behavior of the plants appears in table 3.

Discussion.—In many respects the observations described above are inadequate. No measure was made of the total volume of roots present at any time nor the extent of the root system either in depth or laterally. While the findings recorded may not hold over a longer period of time nor under clipped plots, they do make a starting point for more careful investigation.

Worzella (1932) found a measurable amount of root growth in both the seminal and adventitious roots of Fultz (non-hardy) and Kanred (hardy) wheat between December 2 and February 19, 1930–31. The lowest monthly mean temperature for the three months was 31.5°F. for December. He found no increase in length during this same period in the preceding year when the monthly mean temperatures for December and January were 29.7° and 23.4°F., respectively. He found only a few adventitious roots developing in the fall as compared with spring.

With the grasses, especially rough-stalked meadow grass, timothy, meadow fescue, redtop and perennial rye, there was very active formation of new adventitious roots in November and the first half of December in 1938 and in 1939. The production of new roots continued more slowly with the onset of colder weather and was resumed actively in March. During the second winter only a few new roots emerged from those species with "perennial" root systems. Actual elongation was not measured during those periods when the soil was frozen but the presence of dividing cells was considered evidence that the root tips were growing.

It was assumed that under normal conditions out of doors, the changes in temperature are gradual in comparison with the time required for cell division. Therefore, any cell divisions begun under favorable conditions will continue to completion in spite of lowering temperatures, although new divisions may not be initiated. However, it is recognized that under certain conditions this assumption may be false. When the sun is shining, the air temperature may be below 32°F. and dark objects exposed to the sun many degrees warmer. On such days the roots near the crowns of the plants may reach a temperature where cell division can occur. Then at sunset the temperature of the plant will drop suddenly and some of the dividing cells may not continue to completion. If several following days are cloudy and the temperatures remain uniformly low, the root tips collected during this time will contain cells which are presumably dividing but which are actually "dormant." Further investigation is necessary to determine to what extent cell division is stopped at metaphase by changes in temperature under conditions when mitosis is proceeding very slowly. Other investigators have reported elongation in roots below the frost line or cell division under laboratory conditions at temperatures below the freezing point of water but not in frozen soil. The behavior of root tips which have been "hardened" by exposure to low temperatures may not be analogous with that of root tips under laboratory conditions, and further study is needed here also.

Collison (1935), in upper New York, found apple roots growing below the B horizon on November 20 when the A horizon was 12 inches; B_1, 12 to 23 inches; B_2, 23 to 35 inches; and C, 35 to 47 inches deep, respectively. By December 20, more new roots had developed, some elongating three to four inches. Air temperatures of 3° to 7°F. were recorded during this period. In January and early February, the

TABLE 3

	FEB	MAR	APR	MAY	JUNE	JULY	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY
AIR TEMP-MAX-MIN °F						95-50	85-24	56-14	55-8	45-3	46-8	57-10	62-27	77-35	87-42	100-50
TIMOTHY	+	+ +	● ●	●	+		+	+ ●	●	● +	●	●	●			
NUMBERS OF NEW ROOTS		10-15	2-3 5-10		5-10	0	2-3	5-6 8-10	10-12	5-6 5-6	5-6		20-25	3-5	0	8-10
TIMOTHY-S50	+	+ ●	●		●		●	+ ●	●	● +	●	●	●			
NUMBERS OF NEW ROOTS		50	7-10 0	0	15-25	0	10-12	10-12 40	10-12	5-6 5-6	10-20		20-30	0	6-8	8-10
REDTOP	+	+	● ●		+		+	+ ●	●	+	●	●	●			
NUMBERS OF NEW ROOTS		10-15	2-3 5-6	3-5	1-2	0	2-3	5-8 20	15-20		3-6			0	4	3-4
MEADOW FESCUE	+	●	● ●	●	+	+	●	+ ●	●		●	+	●			
NUMBERS OF NEW ROOTS		3-5	3-5 3-5	0	3-7	10-15	5-6	10-20 8-10	8-10	0	3-4		10-15	0	0	8-10
ROUGH-STALKED MEADOWGRASS	+	+ ●	● ●	●	+	+	+	+ ●	●			+	●			
NUMBERS OF NEW ROOTS		30-40	3-5	0	3-7	10-15		10-15 50	40-50	0	0		40-50		3-4	
PERENNIAL RYEGRASS		●	● ●	●			●	+ ●	●		+					
NUMBERS OF NEW ROOTS	0	0 6-10	3-5 0	0	0	0	3-4	3-4 3-4	5-6	0	1-2	0	0	0	10-12	3-4
KENTUCKY BLUEGRASS	+	+ +	+ +		+	+	+	+ ●	●	●	+	+	+			
NUMBERS OF NEW ROOTS		10-12	6-10 5-10	0	5-10	2-3	2-3	3-4 1-2	2-3	2-3	1-2		12	0	0	
CANADA BLUEGRASS		+ ●	● +				+	+ +	●	●	●	+	●			
NUMBERS OF NEW ROOTS		10-12 15-20	6-10 5-10	0	0	0	2-3	1-2 1-2	2-3	6-8	2-3		3-4	0	0	0
ORCHARD GRASS		●	● ●		●		●	+ ●	●	+	+	+				
NUMBERS OF NEW ROOTS	0	0 5	7-10	0	3-5	0	3-4	4-5	1-2	0	1-2	3	3	0	3-4	3-4
CRESTED WHEATGRASS		+ ●	● ●		+			●	●		+					
NUMBERS OF NEW ROOTS	0	4-5	3-4 1-2	0	1-2	0	0	0 3-4	2-3	0	1-2			0		4-5

+ NEW ROOTS PRESENT SHORTER THAN ONE INCH; ● LENGTH OF NEW UNBRANCHED - HEIGHT OF BLOCK 15 INCHES; FLOWER PRIMORDIA; HEADS ALMOST OUT; HEADS OUT-POLLEN NOT VISIBLE; HEADS OUT-POLLEN PRESENT; HEADS OUT-POLLEN SHED; SEEDS PRESENT

temperature dropped to —21° and even to —31°F. with zero recorded for continued periods but the roots were still growing at the 42 to 54 inch levels. At this time the frost line had reached a depth of 27 to 30 inches. The lower soil temperatures for the B_1, B_2 and C levels were 32°, 33°, and 36°F. in order. These temperatures were fairly constant indicating that the root growth took place at temperatures very close to, if not actually, freezing.

Harris (1926), in the milder climates of Oregon and British Columbia, found that at the five-inch depth there was no growth in apple and filbert roots between December 10 and January 9. At lower levels, 12 to 24 inches, where the temperature was never below 40°F. the growth continued throughout the winter. If the ground water rose and ice was formed over the roots at the five-inch level, only the older roots survived, producing new laterals in February. Under drought conditions during the summer, growth ceased and was not resumed until after the autumn rains.

McDougal (1916), in the more severe climate of Illinois, observed that root elongation of *Acer saccharinum* was most vigorous during May and June, stopped during a drought in July and August and began again in September and October. Slow growth extended into December and no further elongation was noted until the following April. The roots of *Carya laciniosa* grew at the lower level (30 inches) throughout the summer, but no elongation could be observed after November 24. The behavior of *Tilia americana* was like that of *Acer* during the summer, but no elongation occurred after November 24. Growth was not resumed during the following season in any of the three species until April 5. During May and June elongation was especially extensive and with an abundance of rainfall it continued throughout the summer.

Leitch (1916) determined the rate of elongation of roots in freshly germinated seedlings of *Pisum sativum* at various controlled temperatures. She found no elongation at temperatures below —2°C. (28.4°F.). At —0.5°C. (31.1°F.) she observed 0.56 millimeters increase in length over a period of 22½ hours. She did not determine whether elongation at these temperatures was a result of cell division, cell elongation, or both.

The observations of root growth here reported agree more with those of Leitch than with the others. During the winter of 1938–39 and again in 1939–40, frequent dividing cells were found in root tips of grass which had remained in frozen soil for several weeks. All of the root tips examined were short ones in the upper ¾ inch of the soil. Except for periods of less than twenty-four hours, the soil was frozen continually from the last week in December, 1939, until the last of February, 1940. The minimum air temperature for the winter was recorded at 4 A.M. January 10, following a period of four weeks when the maximum temperatures were 53°F. for one hour December 10 and 52°F. for two hours December 4, rarely rising above 40°F. the rest of the time. Maximum temperature for January 10 was 33°F. at noon. The soil was frozen more than twelve inches down, and some of the longer white roots of timothy, which presumably had grown in recent months, were brown at the tips as if injured by cold. When plants were dug at 2 P.M. that same day and root tips emerging from the crowns were fixed and sectioned, dividing cells were found in both varieties of timothy, orchard grass, crested wheat grass and Kentucky bluegrass but not in Canada bluegrass. All the tips were broken in the redtop plant and meadow fescue. The mitotic figures were not so numerous as they were in tips collected at later dates, but they were unmistakably present.

Bouyoucos (1916) found that the temperature of the upper two inches of soil is greatly influenced by the temperature of the air above it, but that once soil is frozen it remains very close to the freezing point. In sunlight the temperature of soil tended to be higher than that of the air since the soil is dark in color and absorbs heat. Opposite sides of a furrow or of a frozen lump of soil with one side exposed to sunlight had greatly different temperatures. The sunny side often thawed while the shaded side remained frozen. Observations of the grass plots indicated that not even the soil surface which was exposed to the sun had thawed January 10, 1940. The temperatures of the crowns of the plants and closely adjacent soil probably remained at subfreezing temperatures for longer periods than at temperatures above freezing during January and February. Leitch noted that the *Pisum* roots exhibited a slight general contraction between —2°C. and —5°C. and "froze" at —5°C. (23°F.), but they elongated normally after being thawed at room temperature. She did not indicate any time factor or temperature at which injury occurred. The actual minimum temperatures at which the cell divisions take place and the time required for the process to go to completion at these temperatures should be studied more carefully.

Martens (1928), basing his opinion on his own observations *in vivo* on young developing stigmas of *Arrhenatherum elatius,* and on the the observations of Jolly with animal tissue, thought that at 19° to 20°C. from 78 to 110 minutes were required for mitosis from the beginning of the prophase to the end of the telophase, not including the time of interphase. DeWildeman (1891) observed the time for mitosis in *Spirogyra* at varying temperatures. At 3° to 4°C. he recorded more than fourteen hours for the completion of the whole process and at 12°C., the optimum temperature, forty-five minutes. Stålfelt (1921) considered observations on living material somewhat questionable, since a change of 5°C. during the process inhibited mitosis. By counting the mitoses in sections of fixed material which had been kept at definite temperatures, he was able to compute the rate of mitosis in *Pisum* roots. At 18°C. from the late prophase to the early telophase he estimated the time to be 11.8 minutes, which is about half of the time determined for these stages by Martens at 19°C.

The cells in the grass root tips may have been dividing slowly at temperatures slightly above and below 32°F. On the other hand, the mitoses may have proceeded intermittently when the crowns of the plants absorbed heat from the sun and the temperatures were warmer than air temperatures. There were probably quiescent periods at night or on cloudy days when the temperature of the plants was much below the 28.4°F. cited by Leitch as the lowest temperature at which elongation occurred. In view of these data, and the very rapid elongation of the roots as soon as the soil thawed in the spring, grass roots are apparently never completely dormant during the winter in Rhode Island. In other regions where the temperatures during the winter months are lower than they are along the New England shore, the roots of perennial grasses may cease growing until spring.

Sprague (1933) compared the root development on established plats of colonial bent and Kentucky bluegrass during April, May, and June. He considered that at least half of the roots he found July 1 had developed during the past three months. These data are in agreement with observations of colonial bent for one year but are contrary to the condition found existing in Kentucky bluegrass. His plats were five-year-old sod maintained at ⅞ inch, whereas the plants described here were not clipped during the two years of the experiment. The treatment of the tops may affect the root growth.

All observers agree that root growth in the upper levels ceases during the summer months. Brown (1939) found that high soil temperatures were more injurious than high air temperatures. Kentucky bluegrass, Canada bluegrass and orchard grass produced an appreciable amount of root growth at 40°F., attaining their maximum growth at temperatures from 50° to 60°F. Orchard grass was more resistant to high soil temperatures than either of the other species. In both Kentucky bluegrass and Canada bluegrass root growth almost ceased in the lower levels with soil temperatures of 80°F. and stopped altogether at 90°F. While orchard grass roots made considerable growth at a soil temperature of 80°F., they suffered very little when the lower soil levels were 70°F., the surface temperatures 93°F. and the air temperature 100°F. At a temperature of 100°F. for both soil and air, the plants died.

The measurements of soil temperature, while not at all complete, show a trend which agrees with Brown's results. The daily soil temperature of the upper two inches when read at noon is approaching the maximum and gives a comparative estimate of that temperature. The average values for the last half of April and the entire month of May, 1939, were 54°F. and 61°F., respectively, which is well within the limits for maximum root growth as found by Brown. The average daily maxima for June, July, and August, 1939, were 71°F., 77°F., and 78°F. which are somewhat lower than the 80°F. at which Brown found root growth practically ceased. The temperatures decreased gradually, and for October the average was 58°F., November 41°F., and December 37°F. During the last week in December, the soil thermometers registered 32°F. every day.

The lowest temperature at which Brown investigated the behavior of grass was 40°F. where he found considerable growth. The observations described here have shown that root growth may actually take place at lower temperatures although extensive elongation probably does not occur when the soil temperature is below 32°F.

The development of the flower primordia which was first noticed about the time the production of new roots ceased may be correlated with the root development. Brown's data show rather conclusively that the growth of roots is largely conditioned by soil temperature, but he did not distinguish between the emergence of new roots and the elongation of existing roots.

SUMMARY

The seasonal development of twelve species of grasses was observed on unclipped plants for two years.

For some of the species the whole root system was regenerated annually, with active production of new growth beginning in October, continuing slowly through the winter and increasing rapidly after the spring thaw in March with its maximum in April. After the middle of June few, if any, new roots were formed and there was no appreciable growth of existing roots until October. Most of the old roots disintegrated shortly after the new ones developed. These species include timothy, timothy S-50, meadow fescue, rough-stalked meadow grass, perennial rye grass, probably colonial bent, and redtop.

With other species the development of the roots during the first year was essentially the same as that described above, but only a small percentage of the roots disintegrated, and after the first spring only a few new roots developed. Most of the new roots developed during the second year were at the nodes of new rhizomes. The species with "perennial" roots are Kentucky bluegrass, Canada bluegrass, crested wheat grass, and orchard grass.

If cell division is a fair criterion of growth, root tips were found dividing at temperatures very close to 32°F.

The cessation of root growth during the summer months coincided with periods of high soil temperatures.

There is some indication that the production of new roots may be inhibited by the developing flower primordia.

Rhode Island Agricultural Experiment Station,
Kingston, Rhode Island

LITERATURE CITED

Bouyoucos, George J. 1916. Soil temperature. Michigan Agric. Exp. Sta. Tech. Bull. 26: 688–816.

Brown, E. Marion. 1939. Some effects of temperature on the growth and chemical composition of certain pasture grasses. Missouri Agric. Exp. Sta. Res. Bull. 299: 1–76.

Collison, R. C. 1935. Lysimeter investigations. IV. Water movement, soil temperatures, and root activity under apple trees. New York Agric. Exp. Sta. Tech. Bull. 237: 1–31.

Evans, T. W. 1939. The root development of New Zealand browntop, chewing's fescue and fine leaved sheep's fescue under putting green conditions. Jour. Board Greenkeeping Res. (Great Britain) 2: 119–124.

Harris, G. H. 1926. The activity of apple and filbert roots especially during the winter months. Proc. Amer. Soc. Hort. Sci. 23: 414–422.

Leitch, I. 1916. Some experiments on the influence of temperature on the rate of growth in *Pisum sativum.* Annals Botany 30: 25–46.

Martens, Pierre. 1927. Recherches experimentales sur la cinesé. La Cellule 38: 69–174.

McDougal, W. B. 1916. The growth of forest tree roots. Amer. Jour. Bot. 3: 384–392.

Sprague, H. B. 1933. Root development of perennial grasses and its relation to soil conditions. Soil Sci. 36: 189–209.

Stålfelt, M. G. 1921. Studien uber die Periodizität der Zellteilung und sich daran anschliessende Erscheinungen. K. Sv. Vet. Akad. Handl. 62: 114 pp.

Weaver, J. E. 1926. Root development of field crops. McGraw Hill Book Co., New York, N. Y.

———, and W. E. Bruner. 1927. Root development of vegetable crops. McGraw Hill Book Co., New York, N. Y.

Wildeman, E. de. 1891. Premières recherches au sujet de l'influence de la température sur la marche, la durée et la fréquence de la caryocinèse du règne végétal. Ann. Soc. Belg. Microscop. 15: 5–58.

Worzella, W. W. 1932. Root development in hardy and non-hardy winter wheat varieties. Jour. Amer. Soc. Agron. 24: 626–637.