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Extent and Longevity of the Seminal Roots of Certain Grasses

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EXTENT AND LONGEVITY OF THE SEMINAL ROOTS OF CERTAIN GRASSES[1]

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(WITH SEVEN FIGURES)

Introduction

Grasses possess two distinct root systems. The primary or seminal root system begins development immediately upon the germination of the seed and consists of one to several main roots and their branches, the number varying with the species. The young plant is entirely dependent upon this primary root system for water and soil nutrients. Later, especially during the period of tiller production, a secondary or nodal root system develops from the lower nodes of the parent culm and from the tillers. The seminal roots are often designated as temporary in general texts and even in special books on grasses. HITCHCOCK (1) states: "The primary root persists only a short time after germination, its place being taken by secondary roots produced from the nodes of the young culm."

It has been observed by LOCKE and CLARK (5) that where extremely dry surface soil or soil drying or crusting prevented normal development of nodal roots, the seminal roots furnished sufficient moisture to maintain the growth of the wheat plant to maturity. WEAVER, JEAN, and CRIST (13), after numerous investigations on the root systems of several cereal crops, concluded that the seminal roots remain alive and active until the time of harvest. SIMMONDS and SALLANS (12) found that the wheat plant may produce seed when dependent almost entirely upon the seminal roots. SIMMONDS (11) states that the seminal roots of wheat remain functional throughout the entire life of the plant. Records on absorption of water and salts from water cultures by KRASSOVSKY (3) have shown that the seminal roots of wheat, barley, and rye are active up to the time of harvest. These findings were later confirmed by plants grown in soil (4). PAVLYCHENKO (9) states that in the several annual grasses studied in arid climates, seminal roots functioned throughout the entire growing season and were frequently the only roots supporting the plant from emergence to maturity.

Studies on seminal roots of perennial grasses, however, are very few, and usually mention of their development is only incidental. The purpose of this study was to ascertain the extent of their development among perennial grasses; how long they remain alive and functional after the secondary root system is established and how much growth grasses can make when supported by the seminal roots alone.

Methods

Wooden boxes 10 × 10 inches in inside width and 24 inches deep were used. They were lined with galvanized iron. One side was removable. It

[1] Contribution from the Department of Botany, University of Nebraska, no. 145.

was held in place by means of two large iron bands and small bolts. The boxes were filled with loam potting soil, previously screened, brought to an approximately uniform water content favorable for rapid growth, and thoroughly mixed. In filling the boxes to within an inch of the top, the soil

TABLE I

DEVELOPMENT OF SHOOTS AND ROOT SYSTEMS OF 14 DIFFERENT NATIVE AND INTRODUCED GRASSES WITH DEGREE OF DECORTICATION OF SEMINAL ROOTS AT DIFFERENT PERIODS OF GROWTH

	Agropyron cristatum (L.) Beauv.				*Agropyron intermedium* (Host) Beauv.			
Age, days	21	41	53	90	21	37	59	96
Av. ht., in.	4.5	10	5	9	5.5	10.5	9	15
Av. no. lvs.	5	6	5	6	4	5	6	7
No. tillers	0	2–7	1–6	12–21	0	2–4	3–4	9–15
No. nodal roots	1–2	5–11	3–9	17–33	2–3	6–8	6–10	36–45
Depth, seminals, in.	7–9	10–22.5	12–15	20.5–23	7–9	18–23	16–23	20–26
Cortex, main root	Intact below 3 inches	Intact below 6 inches	Intact below 4 inches	Intact below 10–15 inches	Intact below 2 inches	Intact below 7 inches	Intact below 4 inches	None
Cortex, branches	Intact	Intact	Intact	Intact below 2 inches	Intact	Intact	Intact	Intact below 4 inches
Root hairs	Abundant at all examinations				Abundant at all examinations			
	Agropyron smithii Rydb.				*Andropogon furcatus* Muhl.			
Age, days	21	41	74	117	21	41	70	110
Av. ht., in.	3	10.5	16	19	1.5	8	8	18
Av. no. lvs.	2	5	7	9	5	7	8	11
No. tillers	0	0	0–2	4–7	0	1–3	1	5
No. nodal roots	1	3–4	6–12	25–32	0–1	4–6	2–10	10–22
Depth, seminals, in.	6–8	16–22.5	10.5–16	19–23	6–8	9–13	10–11	10–14
Cortex, main root	Intact	Intact on lower 6 inches	Intact on lower half	None	Intact below 4 inches	Partially absent except near ends	None except at tips	None except at tips
Cortex, branches	Intact	Intact	Intact	Intact on many finer branches	Intact	Intact except on proximal ends of longer ones	Intact	Nearly intact
Root hairs	Abundant at all examinations				Usually only moderately abundant			

was tamped firmly in place. The top three-fourths inch consisted of loam soil intermixed with an equal volume of sand.

One box was used for each species of grass. The seeds were planted shallowly about 3 inches from each corner of the box and also in the center. Proper watering and mulching promoted prompt germination and good establishment. The seedlings were later thinned to 5 or fewer plants in each of the five areas. Water was applied sparingly so that the soil never became too wet. When roots were to be examined on plants only about three weeks old, no further preparation was necessary since the seminal root could readily be distinguished from nodal roots. But when examination was to be

TABLE I (*Continued*)

DEVELOPMENT OF SHOOTS AND ROOT SYSTEMS OF 14 DIFFERENT NATIVE AND INTRODUCED GRASSES WITH DEGREE OF DECORTICATION OF SEMINAL ROOTS AT DIFFERENT PERIODS OF GROWTH

	Andropogon scoparius Michx.				*Bouteloua curtipendula* (Michx.) Torr.			
Age, days	21	41	73	110	21	37	70	118
Av. ht., in.	1.5	8	9	14	3.5	11	9	18
Av. no. lvs.	5	6	7	9	6	6	5	8
No. tillers	0–1	3–7	2–5	4–11	0–1	3–4	3–4	8
No. nodal roots	1–2	5–7	6–9	18–32	2–3	3–7	5–11	30–38
Depth, seminals, in.	6–8	10–14	11–12	8–12	9–10	14–16	10–15	13–16
Cortex, main root	Intact	Intact below 3 inches	Intact below 2 inches	Nearly intact	Intact below 3 inches	Intact below 6–8 inches	Intact below 5 inches	None
Cortex, branches	Intact	Intact	Intact	Intact	Intact	Intact almost throughout	Intact almost throughout	Intact on some; on others at distal end only
Root hairs	Fairly abundant	Not abundant			Abundant	Abundant	Infrequent on main root, abundant on branches	Present

	Bromus inermis Leyss.				*Buchloe dactyloides* (Nutt.) Engelm.			
Age, days	21	37	61	108	21	41	74	123
Av. ht., in.	5	9	14	16	2	6	4.5	6
Av. no. lvs.	3	5	8	8	5	7	5	8
No. tillers	0	0–1	1–5	Many	0–2	2–11	2–17	17–21
No. nodal roots	2–3	2–6	16–25	Many	0	9–14	4–12	22–33
Depth, seminals, in.	7–8	15.5–23	17–23	18–24	7–8	7.5–14	10–11	12–14
Cortex, main root	Intact	Intact below 6 inches	Intact on lower half	None except on lower 2–6 inches	Intact on lower 2 inches	Intact only on last inch	Intact only near tip	Intact only near tip
Cortex, branches	Intact	Intact	Usually intact	Intact on many; on distal parts of others	Intact	Intact on small branches		
Root hairs	Abundant at all examinations				Abundant at all examinations			

made after 6 to 17 weeks of growth, the seminal roots were banded when about 3 weeks old. In a few grasses where there was more than one seminal root, the one of earliest emergence and greatest length was banded. Banding was facilitated by tilting the box so that after removing the mulch the layer of sandy soil could be carefully washed away with water from a bulb type of plant spray. A small band of very thin, pure sheet tin about 2 mm. wide was gently but rather tightly rolled about each seminal root near its origin. About 20 plants were thus banded in each box, care being taken to

TABLE I (*Continued*)

DEVELOPMENT OF SHOOTS AND ROOT SYSTEMS OF 14 DIFFERENT NATIVE AND INTRODUCED GRASSES WITH DEGREE OF DECORTICATION OF SEMINAL ROOTS AT DIFFERENT PERIODS OF GROWTH

	Elymus canadensis L.				*Elymus junceus* Fisch.			
Age, days	21	41	73	112	21	42	71	110
Av. ht., in.	3	6	10	14	3.5	8	11	11
Av. no. lvs.	3	5	5	7	3	5	6	7
No. tillers	0	3–7	2–5	8–14	0	2–3	2–4	14
No. nodal roots	0–1	9–12	8–21	33–60	2	5–9	6–15	.23–44
Depth, seminals, in.	6–7	16–18	17–24	18–25	7.5–8	8–14	15–23	20–23
Cortex, main root	Intact	Intact	Intact	Intact	Intact	Intact only on last 5 inches	None	None
Cortex, branches	Intact	Intact	Intact	Intact	Intact	Intact below 3 inches	Intact	Only on finest branches and tips of branches
Root hairs	Present	Present	Present	Abundant on branches	Abundant at all examinations			

	Panicum virgatum L.				*Sorghastrum nutans* (L.) Nash			
Age, days	21	37	73	108	22	41	71	110
Av. ht., in.	3	8	16	19	4	15	9	14
Av. no. lvs.	4	6	6	7	4	5	6	7
No. tillers	0	0–3	3	2–12	0	2–3	2–4	9–15
No. nodal roots	2–3	4–5	6–9	21–28	2–4	6–12	5–11	25–40
Depth, seminals, in.	7–8	9–17	12–14.5	11.5–23	7–8.5	9.5–15	10–11	7.5–15
Cortex, main root	Intact	Intact	Intact	Intact	Intact	Intact below 10 inches	Intact on lower half	None
Cortex, branches	Intact	Intact	Intact	Intact	Intact	Intact	Intact	Mostly intact
Root hairs	Usually abundant on branches, fewer on main root				Sparse on main root, abundant on laterals	Infrequent on both main root and laterals	Infrequent	Irregularly distributed; locally abundant

keep the roots moist while banding and to cover them immediately afterward with a dry sandy soil which was then watered.

Examination of the seminal root was made after the side of the box had been removed. Sometimes it was necessary to tilt the box backward to prevent the soil from caving. In earlier stages of growth root excavation was accomplished rather easily with the aid of an ice pick. The main root and all of its laterals were exposed and the depth and lateral spread recorded. Often the entire seminal root system was obtained intact. Usually only the plants in the front of the box were removed during the first examination. The soil that had been removed was replaced by a new lot of soil firmly tamped, after the side and bands had been replaced. The remaining plants continued growth unharmed. But with older plants root examination became more difficult and often extremely so since not only were the seminal roots longer and branched more extensively but also they were intermixed

TABLE I (*Concluded*)

DEVELOPMENT OF SHOOTS AND ROOT SYSTEMS OF 14 DIFFERENT NATIVE AND INTRODUCED GRASSES WITH DEGREE OF DECORTICATION OF SEMINAL ROOTS AT DIFFERENT PERIODS OF GROWTH

	Stipa comata Trin. AND Rupr.				*Stipa spartea* Trin.			
Age, days	21	42	74	123	21	41	73	113
Av. ht., in.	1.5	6.5	4	5	5	13	8	14
Av. no. lvs.	3	4	5	7	2	5	5	6
No. tillers	0	1–2	1–3	6–8	0	0	0–1	1–3
No. nodal roots	0–1	3–4	3–5	6–10	2	3–4	22–24	7–10
Depth, seminals, in.	7.5–8	17.5–27	20–24	20–24	7–8	23–24	4–7	23.5–25
Cortex, main root	Intact	None except near tip	None	None	Intact below 3 inches	Intact only on lower 4 inches	Intact on lower half	Intact only on lower 2–4 inches
Cortex, branches	Intact	Intact	Intact	Intact below 5 inches	Intact	Intact	Intact	Intact except on proximal portions of larger ones
Root hairs	Abundant at all examinations				Abundant at all examinations			

with the rapidly developing and numerous roots of the secondary or nodal root system. Often gentle washing with the bulb spray was used as a supplementary method. Sometimes, despite great care, roots were broken, but always at least several of the twenty available for examination were traced to their ends. Ample material was always available for microscopic examinations which revealed the presence or absence of root hairs and the places and extent of decortication.

Two separate plantings were made; one in spring, which furnished materials for examinations at ages of approximately 21 and 41 days after planting, and another one in late fall. In the second lot of plants the seminal roots were examined at ages of about 70 and 119 days. In spring and summer the seedlings grew in a greenhouse with panels of glass removed from the sides and with windows and ventilators open so that the wind blew through the house. Light was about 40 to 50 per cent. that of full sunshine.

In fall and winter usual greenhouse conditions prevailed except that artificial lighting extended the light day until 10 P.M.

Ten species of native grasses and four species of introduced grasses of great economic importance were grown. Supplementary experiments included wheat and oats. The 14 species are listed in table I where the results of the first experiment are tabulated.

Results

CONDITIONS OF SEMINAL ROOTS AT DIFFERENT AGES

Data in the first two columns under each species in table I are from seedlings planted on May 11 and examined approximately 21 and 41 days later. Conditions for growth were very favorable and the plants developed rapidly. Data in the last two columns are from plants grown from seed sown on, or shortly after, October 21 and examined after approximately 73 and 119 days. Obviously all could not be examined even within the same week; the exact number of days of growth is given for each species. Growth was slower than in the spring, but usually development was further advanced at the first examination of plants started in fall than at the second examination of plants grown in spring.

The data are the average of at least 5 plants and often of 8 to 10 of each species; several plants were examined in order to obtain a composite view of the development and condition of the root systems. The number of leaves is that of the parent culm only. The number of nodal roots is included since it is not only a good criterion of the degree of development of the individual but also reveals something of the importance of the secondary root system in comparison with the primary one. Although the seminal roots usually, but not always, grew more or less vertically downward, their extent is given in depth of soil penetration rather than in length. The cortex is described as intact only when microscopic examination revealed that there was no sloughing below the depth stated. Its cells appeared clear and turgid; the root hairs on it were also apparently normal and functioning. Sometimes large areas of the main root above the intact level also possessed normal and functioning cortex; more often it occurred only in local areas or patches. Normally degeneration of the cortex progressed regularly from the proximal toward the distal end of the main root. Near the root tips usually 1 to 2 inches of cortex remained intact throughout the experiment. Decortication on the branches proceeded in a similar manner but much more tardily than on the main root. The abundance or paucity of root hairs indicated in table I refers only to those portions of the root system with cortex still intact.

FIRST EXAMINATION.—Twenty-one days after planting, when the seedlings were between 1.5 and 5.5 inches high and rarely had a tiller, the roots of all species were between 6 and 9 inches deep. An exception was that of *Bouteloua curtipendula* where they were 9 to 10 inches deep, a fact probably correlated with its very rapid germination. One to 4 nodal roots were present on all grasses except *Buchloe dactyloides*. The cortex was intact in 8 species and absent from the main root only above 2 to 4 inches depth in the others, except for one where it occurred only on the two inches immediately above the tip. This early examination afforded an excellent background for the later studies.

SECOND EXAMINATION.—The grasses were mostly 8 to 10 inches tall and in the fifth- to sixth-leaf stage after 41 days. All but *Agropyron smithii* and *Stipa spartea* had 1 to 4 tillers and certain species as many as 7 to 11. Number of nodal roots had increased greatly. The range in number was from 3–4

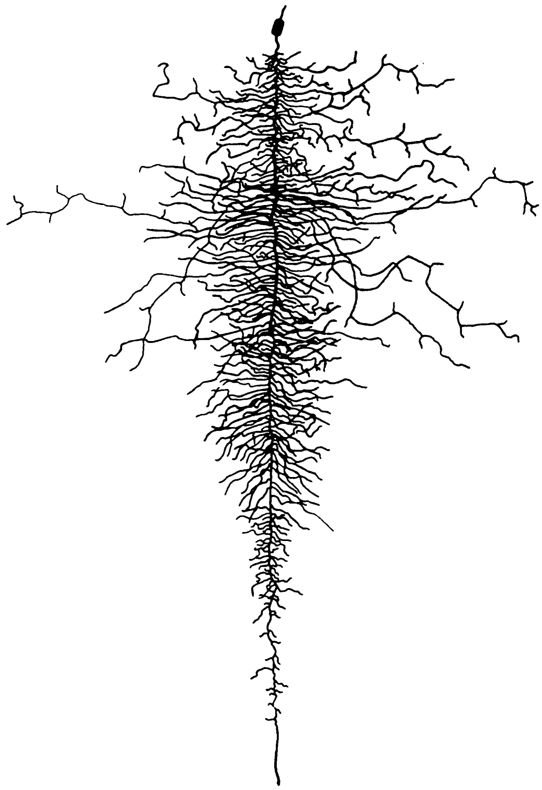

FIG. 1. Seminal root system of *Panicum virgatum* on May 13 grown from seed planted 63 days earlier. The top, which was nearly a foot tall and had 6 leaves, was supported entirely by the seminal root which was 12 inches long, the nodal roots having been repeatedly excised.

to 9–14 and in many of the boxes some of these roots had extended to the bottom. The pattern of the seminal root system, except that the roots were much finer, was in general not greatly unlike that of other grass roots. But as in other root systems, the details of the pattern varied widely among the species. A few examples will illustrate some differences. The light-colored and relatively coarse seminal root of *Panicum virgatum* was always dominant and its branches subordinate. The lateral spread was relatively small (fig. 1). The dark-colored and extremely fine seminal root of *Buchloe* *dactyloides* held its course definitely, penetrated downward nearly vertically, and was not easily confused with its major branches. The dark-colored seminal root of *Andropogon furcatus* branched widely not only in the surface soil but also at greater depths (fig. 2). Conversely, the light-colored seminal root of *A. scoparius,* while profusely branched throughout its course, had, except in the surface 2 inches of soil, branches that were rarely over 1.5 inches long. The seminal roots of *Stipa comata* had relatively few long branches and even short ones were not abundant. *Bouteloua curtipendula* had seminal root branches which were very long and extremely fine, often being cobweb-like in appearance. The seminal roots of *Agropyron intermedium* were also extremely fine, often being almost invisible against the background of dark-colored soil. The quality of fineness of the seminal roots aided greatly in preventing confusing them with portions of nodal roots.

The seminal roots, when measured one-half inch below the seed, varied in diameter with the species and with decortication from 0.3 to 0.1 mm. Exceptions were roots of *Sorghastrum nutans* (0.33 mm.) and *Stipa spartea* where a diameter of 0.6 mm. was found. In some grasses the seed coat remained in place for a long time and continued to show clearly the place of origin of the seminal root. *Stipa spartea* and *Bouteloua curtipendula* are examples. The seed coats of *Buchloe dactyloides* and certain others were still undecayed 73 days after planting.

The shallowest seminal roots when 41 days old were those of *Andropogon scoparius, A. furcatus, Buchloe dactyloides,* and *Elymus junceus.* They were only 7.5 to 14 inches deep. The deepest were those of *Agropyron intermedium, Stipa spartea,* and *S. comata,* which either extended to or ran along the bottom of the box. Some nodal roots of all species were abundant in the first foot of soil and in most species they also reached the maximum depth of the soil. The cortex on the main root was either entirely intact (2 species), intact below 3 to 10 inches depth (6 species), or absent except on 1 to 6 inches of the distal end, as in *Agropyron smithii,* both species of *Stipa, Andropogon furcatus, Buchloe dactyloides,* and *Elymus junceus.* None of the branches were decorticated, except a small part on their proximal ends in *Andropogon furcatus* and *Elymus junceus,* but only the smaller branches of *Buchloe dactyloides* retained the cortex.

THIRD EXAMINATION.—The age of the plants at this examination ranged from 61 to 74 days, except that of *Agropyron cristatum* and *A. intermedium* which was 53 and 59 days old, respectively. Grasses of intermediate height were 8 to 11 inches tall. A few, including *Buchloe dactyloides* and *Stipa comata,* were only 4 to 5 inches high, but others, as *Bromus inermis,* were 14 to 16 inches tall. The leaf-stage ranged from the fifth to the eighth. Plants of all species had at least 1 tiller, 2 to 4 were common, but *Buchloe dactyloides* possessed 2 to 17. In five of the boxes the tillers were about two-thirds as tall as the parent plant. In five, they were about half as tall; but those of *Agropyron intermedium* and *Bromus inermis* were as high as the parent culms. Many new nodal roots had developed. The fewest were 3 to 5

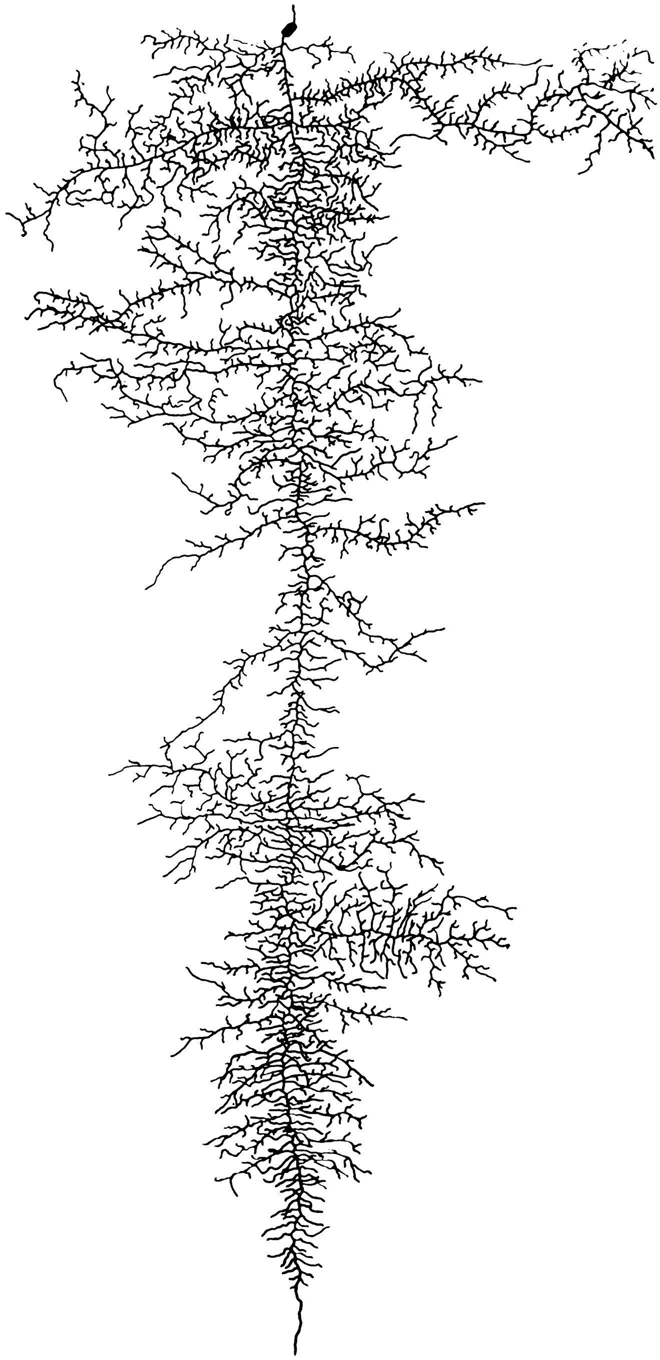

FIG. 2. Seminal root system of *Andropogon furcatus* on May 20, grown from seed planted 70 days earlier. The depth is 21 inches. The top grown on this root alone is shown in figure 3.

(*Stipa comata*); 6 to 10 were frequent; but some plants of *Elymus canadensis* and *Bromus inermis* had 21 and 25, respectively.

Depth of root penetration varied from 10 to 24 inches. Some species were no more deeply rooted than at the second examination in spring. The cortex on the main root of *Elymus canadensis* and *Panicum virgatum* was intact; on four other species it was intact below 2 to 5 inches. But on *Elymus junceus* and *Stipa comata* there was none. It occurred only near the root tip in *Buchloe dactyloides* and *Andropogon furcatus,* but over the lower half of the root of plants of four other species. Cortex of the branches was entirely or almost entirely intact on all but *Buchloe dactyloides*, where it remained regularly only on the smaller branches.

FOURTH EXAMINATION.—At the final examination the various grasses ranged in age from 90 to 123 days (table I). They were well developed. Many were 9 to 15 inches tall but several were 18 to 19 inches in average height. The number of leaves had increased; there were mostly 7 to 9. Except for the sod-forming *Agropyron smithii* and the slow-growing *Stipa spartea,* the number of tillers ranged from 5–8 to 17–21 per plant. The abundant tillers were often as tall as the parent culm. *Bouteloua curtipendula* and *Panicum virgatum* were in blossom and the bunches of *Buchloe dactyloides* with stolons 4 to 20 inches long had the appearance of mature plants.

This examination was the most difficult since the number of roots of the secondary root system had greatly increased. Twenty to 30 roots per plant were common, except for species of Stipa where 6 to 10 prevailed. Plants of *Elymus canadensis* and *Agropyron intermedium* possessed 33 to 60 each. Most of the seminal roots now extended deeply and frequently to the bottom of the box. They were intermixed with the nodal roots throughout much or most of their course.

The cortex was intact throughout in *Elymus canadensis* and *Panicum virgatum,* nearly intact in *Andropogon scoparius,* and not degenerated below 10–15 inches in *Agropyron cristatum.* It occurred only on the lower 1 to 6 inches of the roots of *Andropogon furcatus, Bromus inermis, Buchloe dactyloides,* and *Stipa spartea.* On the six remaining species there was none. Cortex on the branches was nearly or entirely intact on the first four species noted above, where the same condition prevailed on the main root of three of these species. This condition of the branches maintained also in *Agropyron intermedium, Andropogon furcatus, Sorghastrum nutans,* and *Stipa comata.* Conversely, cortex was found only on many of the finer branches of the remaining species. The surface of the main seminal root composed only a very small portion of the entire absorbing surface of the greatly branched root system. Even if it and the proximal portions of the major branches were decorticated the root probably could still absorb and transport water and solutes at nearly its former capacity.

Judging from the macroscopic appearance of the relation of the seminal roots to the soil, in conjunction with extensive examinations of numerous portions of the roots under the microscope, it appeared that the extent of physiological activity in the several species at this last examination was quite different. In *Elymus junceus* it seemed that all of the roots were nonfunctional as absorbing organs except near the root tips. Perhaps only one-third of the entire root surface was active in absorption in *Agropyron intermedium, A. smithii, Bouteloua curtipendula,* and *Buchloe dactyloides.* It seemed clear that the absorbing surface was considerably greater in the remaining species where one-half to two-thirds of the entire root system appeared to be intact. Much information was gained about longevity and activity of the seminal roots in later experiments in which development of the secondary root system was prevented and the plants were supplied with water and nutrients by the seminal roots alone.

Maximum depths of penetration

Since many of the seminal roots reached the bottom of the boxes, a new lot of each of four species of grasses was grown in boxes of the same surface area but 4 feet deep. Seeds were planted in March or April and the seminal roots were banded when the seedlings were in the second-leaf stage. The seminal roots of *Stipa comata* 77 days after planting were growing vigorously and showed no decortication. Depths of penetration varied from 17 to 20.5 inches on five plants. Some roots of the secondary root system penetrated to about the same depth. Roots of *Agropyron intermedium* when 70 days old were traced to depths of 32 to 36 inches. After 46 days the seminal roots of *Panicum virgatum,* which were in excellent condition throughout and apparently still elongating, were 18.5 to 19 inches deep.

From the foregoing experiments it may be seen that the seminal roots of these grasses reached depths of 2 to 3 feet, although some did not extend much deeper than 1 foot, at least during the first 70–119 days of their growth.

Development of plants grown on the seminal root

Grasses of each of four species were grown on the seminal root system alone, roots of the secondary system being repeatedly excised. The seedlings were grown in boxes of soil as described and the seminal roots were banded after they were established. A flat cork, 2.25 inches in diameter and one-fourth inch thick, with a small hole in the center was partly cut and then broken into halves and inserted tightly about the root just below the band, the root occupying the central opening. The cork was held together by a copper wire, and fastened in place in the soil by two long nails inserted through holes on opposite sides from the center. Corks and roots were then covered with a mixture of sand and loam which was kept moist by daily sprinkling. The cork furnished a firm support for the delicate root. By supporting the top, the cork could easily be washed free from soil by means of a fine spray, after the box was properly tilted. New roots, which were continuously produced, grew along the surface of the cork. They were removed by means of a dissecting scissors or razor blade. One could thus be certain that the seminal root alone was left intact. The first two examinations were made at intervals of 18 days, later ones weekly. Data were obtained from 4 or 5 individuals of each species, but only those of representative plants are presented.

Andropogon furcatus, Sorghastrum nutans, and *Stipa spartea* were grown 77 days, from March 11 until May 27, and *Panicum virgatum* until May 13. *Andropogon furcatus* attained a height of 8.5 inches and developed 11 leaves. All the leaves were green and thriving, except the two lower ones which were reddish and dying. *Sorghastrum nutans* had 6 good leaves

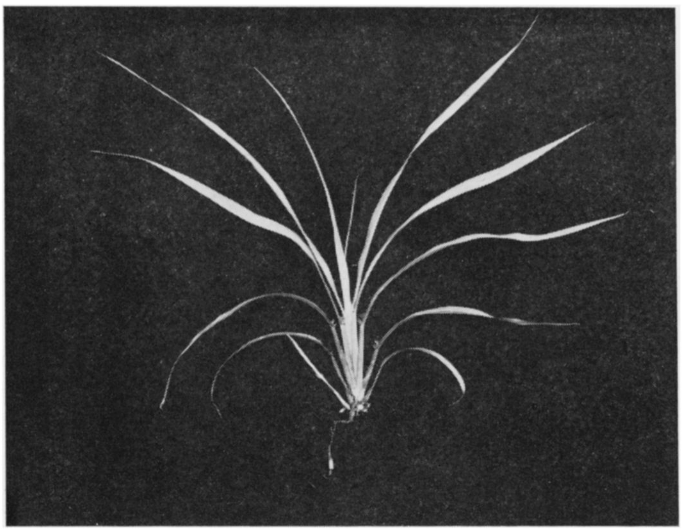

FIG. 3. *Andropogon furcatus* grown on root shown in figure 2. It is 8 inches tall and all but two of the leaves are green and thriving. Note single seminal root and band.

and two dead ones. It was 9 inches tall. The longest of the 8 leaves of *Stipa spartea* extended upward 14 inches. Several of these leaves occurred on the two vigorous tillers. A 63-day-old plant of *Panicum virgatum* had 6 leaves and was 11.5 inches tall.

During the period of growth 20 roots with an aggregate length of 32 inches had been removed from a representative plant of *Andropogon furcatus.* In addition to 29 roots totaling 54 inches in length, several small rhizomes had been excised from *Sorghastrum nutans.* Root production was less in *Stipa spartea* (13 in number and 6 inches in aggregate length) and *Panicum virgatum,* which produced 10 roots averaging an inch in length and also a few rhizomes. In addition to the preceding, a single volunteer plant of *Andropogon scoparius* was grown on its seminal root from June 25 until October 1.

Buchloe dactyloides was grown on the seminal root for two months, June 1 to August 1. The plants tillered profusely, never showed signs of water shortage, and even produced stolons, despite the fact that the diameter of the single seminal root was only 0.18 mm. (fig. 4). The abundant foliage consisted of 137 leaves varying in length from 0.75 to 3.5 inches, only 14 of which were dead.

Longevity of plants grown on seminal roots

Plants of four species of grasses were grown on the seminal root from June 1 until they succumbed, or until October 1. About two weeks after planting and when the seminal root system was well established, the tops of the plants were fastened to vertical supports and the surface soil carefully washed away so as to expose the upper portion of the roots. Thus, the origin

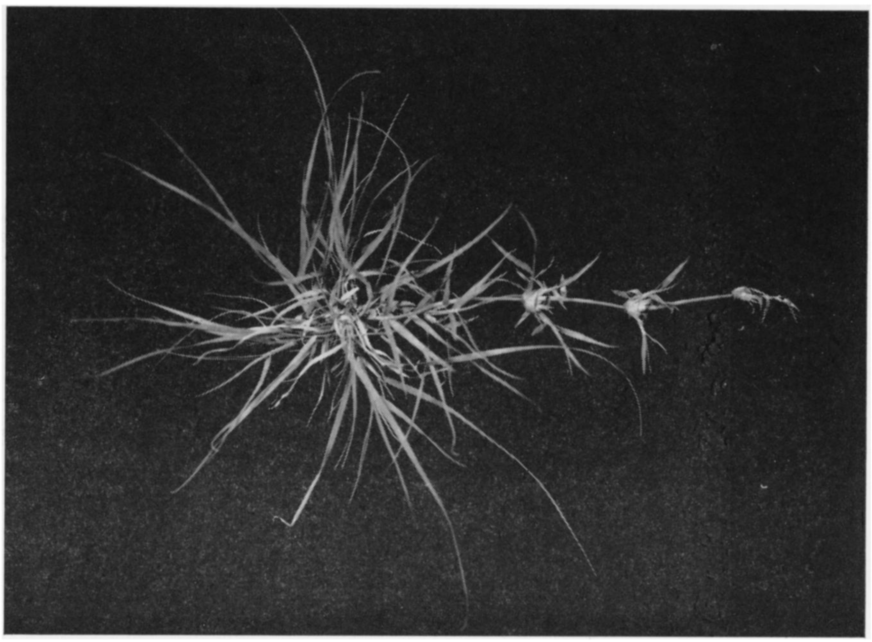

FIG. 4. Single plant of *Buchloe dactyloides* (viewed from above) at the age of 2 months. It was grown on a single seminal root. The stolon is 5 inches long and the leaf area is approximately 20 square inches.

of new roots could be seen. The plants were observed daily and new roots excised as rapidly as they were produced. Conditions favorable to growth were maintained constantly.

These seedlings of *Andropogon furcatus, Sorghastrum nutans, Bouteloua gracilis,* and *Panicum virgatum* had made an excellent growth by July 18. Heights were 10.5, 13, 7, and 10.5 inches, respectively. Among selected representative plants, seven leaves occurred on the parent culm of *Andropogon furcatus* and 3 to 5 on each of the four tillers, a total of 22 leaves. *Sorghastrum nutans* was even better developed. *Bouteloua gracilis* had a total of five tillers and 23 leaves. *Panicum virgatum,* likewise, had tillered freely but most of the foliage (6 leaves) was on the parent culm. A few plants of each species died late in July and all of *Bouteloua gracilis* had succumbed by August 1. Several plants died during the second week in August when severe conditions promoting high transpiration prevailed. Temperatures of 95° to 100° F. were maintained under a clear sky, relatively low humidity, and high wind. At this time a representative plant of *Andropogon furcatus* had a transpiring area of 12 sq. in. (fig. 5). New roots were initiated in large numbers, but they were removed daily. This continued throughout August but at a decreased rate. Contact with the soil was unnecessary for root production. Such contact promoted the process when the

FIG. 5. Plants developed on the seminal root only when 2 months old on August 1. *Andropogon furcatus* (left) is 11 inches tall; *Sorghastrum nutans* (center) has 5 broad leaves and three leafy tillers; and *Panicum virgatum* (right) is well developed and vigorous.

surface soil was constantly moist and humidity was most favorable for their growth. The base of the plant often became somewhat enlarged as a result of repeated removal of roots. The plants remained alive and mostly green during August. Some produced a few new tillers as the older ones died. Late in August a single plant of *Panicum virgatum* developed a small panicle with four spikelets. The flowers remained in blossom two to three weeks. The plant was 11 inches tall and the largest of its four tillers was 6 inches high and possessed 7 leaves. It obtained all of its water and soil nutrients through a single seminal root only 0.3 mm. in diameter.

In September there was little or no further growth and considerable degeneration occurred. The green color was gradually replaced by one of reddish brown or yellow as is usual in the fall. Only one or two plants of each species remained alive on October 1, but they were turgid and not wilted.

Experiments with wheat and oats

Seeds of Marquis spring wheat (*Triticum aestivum* L.) were planted on April 8 in boxes 4 feet deep; four plants were grown in each of two boxes.

FIG. 6. Single plant of Marquis spring wheat (left) 66 days old from which the nodal roots had been excised at weekly intervals. (Right) Control and experimental plants of Kherson oats 49 days old. The plant on the right, which is 28 inches tall, had its nodal roots removed weekly.

The seminal roots were banded 18 days later and nodal roots were removed from the plants in one box at weekly intervals until the seminal roots were excavated on June 13. The plants in the other box were grown as controls.

A representative experimental plant was 25 inches tall when in the post-blooming stage on June 13. There were seven tillers, two with spikes in enclosing leaf sheaths (fig. 6). The experimental plants were so similar to the controls that the only measurable external difference was that they were about two inches shorter. This is remarkable since they had suffered the loss of an average of 51 roots. Some of these were short and unbranched but many were 3 to 5 inches long (the growth of a single week) and well supplied with branches.

An examination showed that all of the main seminal roots and a few of their longer branches had attained depths of 36 to 39 inches and that four of the main seminals had reached the bottom of the box, a depth of 48 inches. This was 10 to 23 inches deeper than seminal roots on the control plants, where an average of 48 roots of the secondary root system also occurred.

Decortication had occurred on the main seminal roots and at least on parts of their large branches to a depth of 20 inches. But the finer branches still appeared fresh and active even in the surface soil, and those of intermediate size below a depth of 6–8 inches. Very similar conditions of moderate deterioration of the upper part of the seminal root system prevailed on the control plants. Below 20 inches depth (14 inches on the controls) the seminal root system was covered with a good cortex and abundant root hairs. The roots appeared fresh and active; in fact, they were much younger than the portions above. Where the seminal root system alone occupied the soil the main roots and their main branches were not only deeper but their laterals branched more profusely, and the branches were longer and more rebranched. Roots were common even in the deepest portion of the soil.

Kherson oats (*Avena sativa* L.) was planted, the seminal roots banded, and nodal roots excised weekly as in the experiment with wheat. When blossoming began on May 27, representative experimental and control plants were 28 and 32 inches tall and possessed 2 and 3 tillers, respectively (fig. 6). Although an average of 21 roots, many of which were 2 to 5 inches long and well branched, had been removed from each experimental plant, there had been no visible wilting at any time. Each plant in both boxes produced but a single panicle.

The seminal roots of plants grown without a secondary root system reached depths of 24 to 26 inches. One of the three seminal roots of such a plant was removed in its entirety from the soil and a diagram made of the position of each main branch. It was then placed in water, the branches properly arranged on black ruled paper, and the entire root drawn to scale without reduction (fig. 7). The presence of an intact cortex with a very large supply of living root hairs below 14 inches where all parts of the root system was apparently functioning was quite significant. The stem just above the seminal roots was 1 mm. in diameter and each of the decorticated seminal roots had a diameter of only 0.2 mm. Branches in the upper 14 inches of soil were mostly decorticated except at their distal ends. But they formed a network, almost cobweb-like in nature, where the minute branches threaded the soil. An abundance of clear, turgid root hairs indicated that they were still active in absorption.

On the controls most of the seminal roots were only 17 to 19 inches deep,

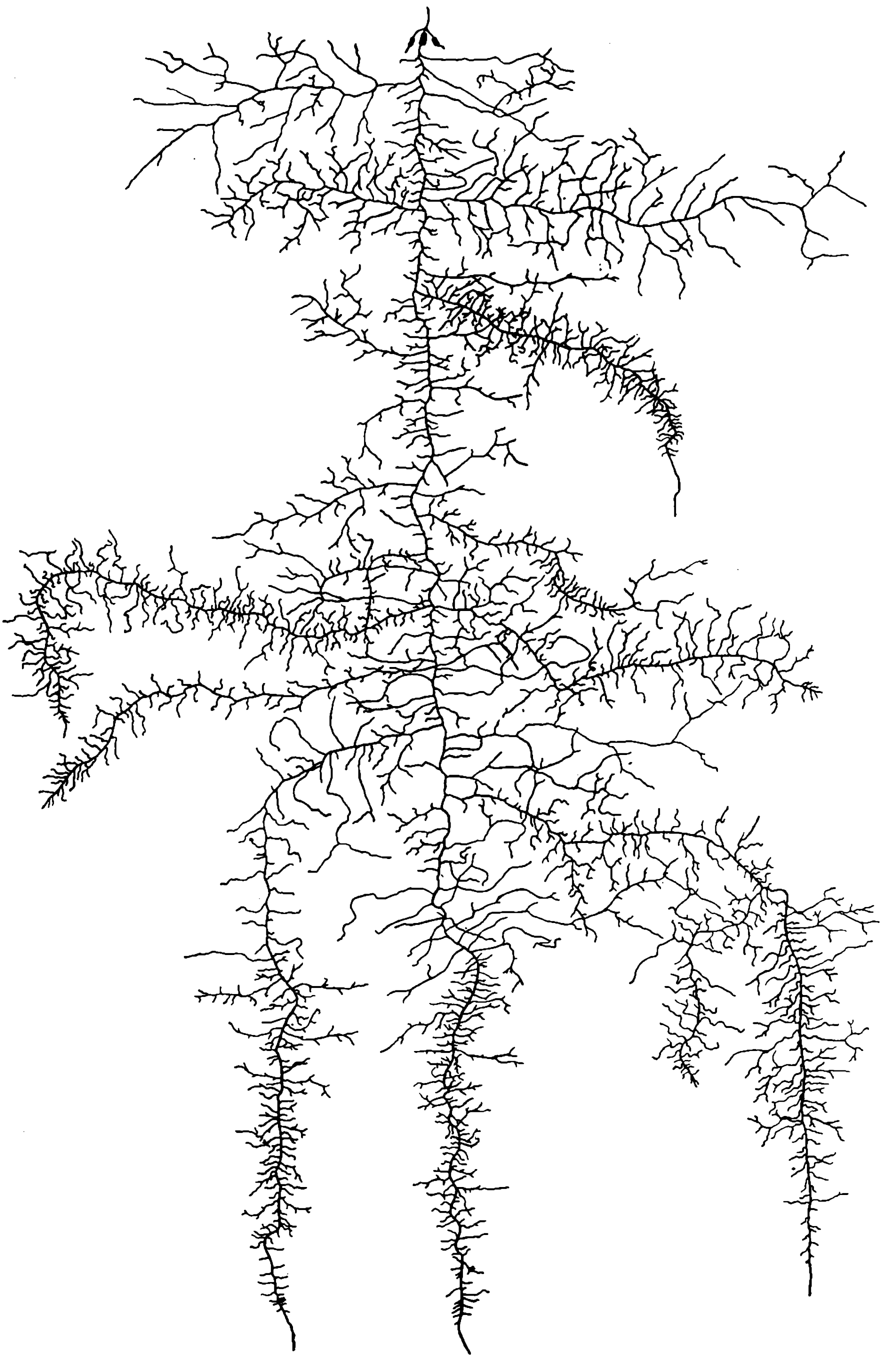

FIG. 7. One of three seminal roots of the plant of Kherson oats shown in figure 6. It is two feet long.

but one extended downward, 34 and another 44 inches. Many of the numerous roots of the secondary system penetrated to the bottom of the box. Decortication of the main seminal roots and their long branches had proceeded farther on the control plants, usually to within a few inches of their growing tips. Compared with the plants with nodal roots removed there were fewer lateral branches, the branches were shorter, and they were not so extensively rebranched. No dense network of branches was found on the controls, although the younger main branches in the deeper soil were abundantly supplied with poorly branched laterals.

Discussion

In all species of perennial grasses studied the seminal root extended 6 to 10 inches in depth during the first 21 days after planting and 7.5 to 27 inches after 41 days. It continued vigorous growth at least until some nodal roots had reached depths of 16 to 24 inches. Depth had increased but little at 59 to 74 days but practically all of the seminal roots were functioning at a time when the abundant tillers were one-half to two-thirds or even fully as tall as the parent culm.

One to 4 nodal roots developed on the parent culm of nearly all of the grasses before tillers appeared. Plants with seminal roots alone not only developed normal, leafy parent culms 8.5 to 14 inches tall but also produced several to many tillers.

Working with *Agropyron cristatum, A. pauciflorum,* and *Bromus inermis,* PAVLYCHENKO (**9**) states that the nodal roots supported these perennial grasses within two months after emergence. In the present studies the seminal root systems of all of the grasses were alive at the end of 4 months and at least partly functional. Seminal root systems alone also supported plants of several species for a period of 4 months. OLMSTED (**6, 7**) states that with adequate establishment of adventitious roots of *Bouteloua curtipendula,* the seminal root probably becomes nonfunctional when 6 to 10 weeks old. His plants were grown in two-gallon jars, 9 inches deep. When they were watered at 12- and 20-day intervals, the primary roots remained alive 4 months and in some plants (33 of the 220) it persisted as the only functional part of the root system. In length (7 to 10 inches) and degree of branching in individual plants seminal roots showed a strong inverse correlation with the numbers of functional adventitious roots.

The seminal roots of perennial grasses are not temporary. They remain alive and active 3.5 to 4 months, and possibly under natural field conditions where growth of seedlings is much slower throughout the first season of growth.

The depth of penetration of the seminal root system of several of the smaller cereals has been shown by WEAVER, JEAN, and CRIST (**13**). These roots often penetrated to the greater depth (approximately 6 feet), the nodal roots massing nearer the surface soil. WEAVER, KRAMER, and REED (**14**) found that the seminal roots of winter wheat grew at the average rate of over half an inch per day during the first 70 days and constituted half of the absorbing area. PAVLYCHENKO (**8**) has traced the development of the seminal root system of wild oats (*Avena fatua*), wheat, rye, and barley, and thus revealed the rapid rate of growth and the total length of the seminal root system. This length ranged from 690 feet in Marquis wheat to 971 in Hannchen barley. He also pointed out the value of the seminal roots in competition with weeds.

HOWARD (**2**) states that on the black soils of India: "The upper soil dries so rapidly after sowing that there is hardly any development of the secondary root system, and practically no tillering. The crop develops slowly on the primary roots." The fact that the weekly removal of the nodal roots of wheat apparently had little effect upon the development of the parent culm is in agreement with the findings of KRASSOVSKY (**4**) who states that the removal of the nodal roots of barley has little influence upon the development and yield of the main stem. She found that "of the plants subjected to a severe wilting at the time of heading, those possessing seminal roots only recovered better than those possessing nodal roots only." OLMSTED (**7**) states that the imposition of a moderate drought probably tends to prolong the life of the primary root system of *Bouteloua curtipendula.* SALLANS (**10**) found that the individual root which contributes most to the final yield of wheat is the primary seminal root, while the first pair of lateral seminal roots is of almost equal importance. KRASSOVSKY (**3, 4**) states that the seminal roots absorb almost double the amount of water per unit dry weight in comparison with the nodal roots. She also states that "the correlation between the time of maximum activity of the seminal roots and the maximum growth of the main stem . . . seems to prove that the seminal roots supply principally the main stem; the nodal roots, the tillers. Removal of the seminal roots in the stage of heading also decreases the yield of the main stem proving that at this stage the barley plant is still dependent on its seminal roots."

Summary

A record was obtained of the development of both roots and tops of 14 species of native and introduced perennial grasses at four stages of growth.

Seminal roots were 6 to 10 inches deep 21 days after planting. There were 1 to 4 nodal roots but rarely a tiller. Twenty days later, when the grasses were mostly 8 to 10 inches tall and well tillered, seminal root depth was 7.5 to 27 inches, and nodal roots were often equally deep.

Seminal roots were usually very fine and the main seminal mostly 0.3 mm. or less in diameter. Branching and length of branches varied greatly among the several species; nearly all were profusely branched. Little or no decortication of the main root had occurred, except in six species where cortex remained only on the distal end. With one exception, cortex of the branches was practically intact.

After 53 to 74 days, when the plants were 5 to 16 inches tall, there were many deeply penetrating nodal roots and numerous tillers one-half to two-

thirds the height of the parent culm. Seminal root depth was 10 to 24 inches. On the smaller branches, and usually on the larger ones, the cortex was intact, but it had sloughed from some of the main seminal roots.

At 90 to 123 days, when the grasses were 9 to 19 inches tall and those of two species had blossomed, the seminal roots, despite 6 to 60 nodal roots, extended deeply and frequently to 24 inches depth. Microscopic examination indicated that, with one exception, about one-third of the seminal root surface appeared normal in one small group, but on the remaining species half to two-thirds of the root system remained intact.

Maximum penetration of seminal roots of 24 to 36 inches was ascertained in certain species. Normally developed plants of several species grew 77 days to heights of 8.5 to 14 inches on the seminal root alone. One plant developed 20 square inches of leaf surface in 60 days on a single, hair-like seminal root. Plants of three species from which all nodal roots were continuously excised tillered freely and remained alive 4 months.

Seminal roots of wheat, with nodal roots excised weekly, were, after the period of blossoming, 3 to 4 feet deep, which was 10 to 23 inches deeper than those of control plants. Similarly, seminal roots of oats usually penetrated deeper than those of the controls. In both species branch roots also penetrated deeper and rebranched more than those of the controls.

Seminal roots of the smaller cereals are not temporary. Those of 14 perennial grasses were usually deep and spread widely. They remained alive and active as absorbing organs 3.5 to 4 months.

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