Seedling Morphology and Seeding Failures with Blue Grama[1]

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Highlight

Morphological differences between seedlings of blue grama and crested wheatgrass show why plantings of blue grama fail while those of crested wheatgrass succeed. When both species are planted at a depth of 18 mm, crested wheatgrass initiates adventitious roots at the depth of planting and blue grama initiates adventitious roots at an average of only 2 mm below the soil surface. Adventitious roots of blue grama usually die in the harsh environment at this shallow depth.

Blue grama (*Bouteloua gracilis* (H. B. K.) Lag.) is a dominant perennial grass on several million acres of the Great Plains. Nevertheless, if judgment regarding its adaptability to the Shortgrass Plains of Colorado were based on the results of seeding trials, it would be rated as not adapted (McGinnies et al., 1963; GP-6 Technical Committee, 1966). This paradox imposes two questions: 1. Why do blue grama seedings fail? 2. Does blue grama spread naturally by seed to unoccupied areas?

Regarding question 2, it is known that blue grama revegetates abandoned plowed fields and severely deteriorated pastures very slowly (Savage, 1939; Riegel, 1941). Savage based his conclusion on a survey of over 160 fields in the Central and Southern Great Plains. Riegel reported on work done near Hays, Kansas. Their conclusion was easily substantiated in 1970. On the Shortgrass Plains of Colorado, abandoned fields have remained in the early *Aristida* stage of secondary succession for the last 20 years. In some places, 40-year-old plow lines were still defined sharply by the line of unplowed blue grama sod. In other places, fields plowed once or twice often retained a few scattered sods of blue grama. Now these residual plants appear as sod "islands" generally less than 1 m across. Since we seldom find small satellite clumps around the "islands," we accept the conclusion that blue grama does not spread readily by seed. Nevertheless, seed production and quality are good enough to suggest that blue grama should play a dynamic role in secondary succession.

Blue grama generally emerges quickly and abundantly from seed planted in moist, warm soil. The problem comes later. Blue grama seedlings die at 6 to 10 weeks of age. A notable exception of good blue grama survival on Shortgrass Plains was reported by Bement et al. (1961). In that case the seeded rows were covered with a thin layer of asphalt emulsion mulch. More recently, when planted in firm, ridged seedbeds (Hyder and Bement, 1969; Marlatt and Hyder, 1970; Hyder and Bement, 1970), seedings of crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult.) succeeded while those of blue grama failed. Morphological differences between seedlings of these two species show why one succeeds and the other fails. The main point of interest is the depth of adventitious rooting.

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Weaver and Zink (1945) reported that blue grama seedlings grown without adventitious roots died in 8 weeks. As a rule, the seminal roots of perennial monocotyledons live only a short time. Thus, plant establishment requires the development of adventitious roots (Esau, 1960). It is not surprising that adventitious roots fail to grow in dry soil (Taylor and McCall, 1936; Boatwright and Ferguson, 1967; Riegel, 1941); but why should blue grama fail to extend adventitious roots, which are essential for survival?

There are two forms of grass seedling growth. One form has an elongated first, or sub-coleoptile, internode. The second form does not have an elongated sub-coleoptile internode, but generally has a long coleoptile and may have an elongated second, or intra-coleoptile, internode. The first form will be called the "panicoid type," and the second form the "festucoid type" (Boyd and Avery, 1936; Sargant and Arber, 1915). Anatomical differences led to additional type characterization (Sargant and Arber, 1915), but the presence or absence of an obvious sub-coleoptile internode is sufficient identification of external morphological form. We follow the advice of Boyd and Avery (1936) by rejecting the incorrect terms mesocotyl (sub-coleoptile internode) and hypocotyl (intra-coleoptile internode).

The coleoptile serves to force a way upward through the soil while protecting the plumule bud within it. Thus, the coleoptile is the structure of grasses adapted specifically for seedling emergence. Foliage leaves are poorly adapted to force themselves through the soil above the reach of the coleoptile. Consequently, depth of planting should not exceed the reach of the coleoptile. Species having very short coleoptiles would need to be planted so shallow that they would be susceptible to the hazards of severe environmental fluctuations near the soil surface, unless they exhibited the characteristic of elongated sub-coleoptile internode. In this case, the reach of the coleoptile above planting depth is the total length of sub-coleoptile internode and coleoptile. The narrow band of meristematic tissue located at the upper end of the sub-coleoptile internode (Boyd and Avery, 1936) is better adapted to pushing the coleoptile upward than would be the long band of meristematic tissue at the lower end of internodes produced above the coleoptile.

Elongation of the sub-coleoptile internode elevates the coleoptilar and higher nodes, from which adventitious roots develop. (To be completely correct, we must add that adventitious roots also may arise from internode tissues.) The depth from soil surface to origin of adventitious roots is determined largely by the length of the coleoptile. Short coleoptiles may place the origin of adventitious roots very near the soil surface.

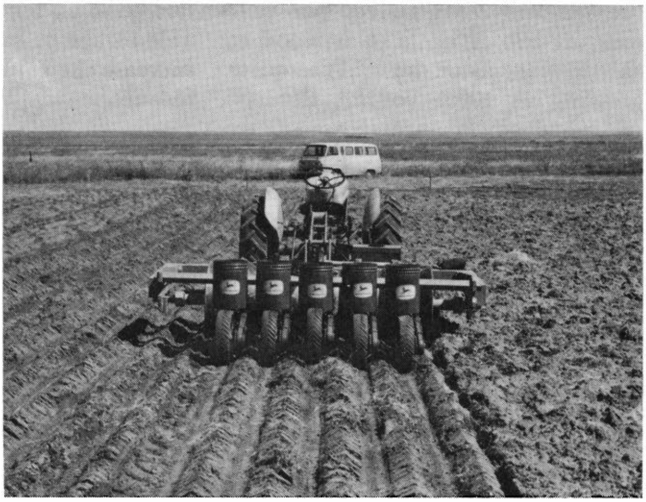

FIG. 1. A ridged seedbed after plowing, packing, and planting.

Since festucoid-type seedlings do not have elongated sub-coleoptile internodes, the lowermost adventitious roots arise near planting depth from or near the coleoptilar node. Sometimes these seedlings elongate in the intra-coleoptile internode. (In fact, such elongation may include more than one internode.) This elongation elevates the plumule and the nodes thereof, from which additional adventitious roots arise.

Obviously, adaptations that facilitate seedling emergence, even though modified somewhat by planting depth, determine the depths of adventitious rooting and affect the process of plant establishment. Since the literature lacks some of the definitive information needed about individual species, we will describe the particular morphology and susceptibility of blue grama seedlings to mortality and compare them with crested wheatgrass.

Methods

Blue grama and crested wheatgrass were seeded with double-disc flexiplanters to a depth of 18 mm in furrows of firm, ridged seedbeds (Fig. 1) in 1965 to 1968, inclusive. Seedbed preparation and seeding were done only when the soil was moist from recent rain, according to the advice of Fults (1944). The system of plowing, packing ridges, and drilling is described in papers previously cited. The densities of established stands are reported in this paper.

Because of nearly complete mortality of blue grama seedlings, we studied morphological development of the grasses in 1967 and 1968. Soil cores 5 cm in diameter and 30 cm deep were cut in seeded rows to obtain seedlings at various stages of development. The soil was washed away with a fine spray of water. Grass seedlings were dried in a plant press, painted black, and mounted on white paper for photographing.

To obtain complete plants for measuring, blue grama and crested wheatgrass were grown in the greenhouse. The sandy loam soil taken from the vicinity of the field trials was moistened, placed in plastic tubes 25 mm in diameter, and firmed to uniform density. Twenty seeds of each species

Table 1. Number of established plants (mean and standard deviation) per foot of row after planting at different times.

Date of planting	Crested wheatgrass	Blue grama
September 20, 1965	1.4 ± 0.4	–
June 10, 1966	1.0 ± 0.2	–
April 12, 1967	2.8 ± 0.8	0.4 ± 0.1
May 11, 1967	1.7 ± 0.4	0.2 ± 0.1
June 6, 1967	1.1 ± 0.2	0.3 ± 0.1
September 1, 1967	0.8 ± 0.2	0.1 ± 0.1
May 2, 1968	1.2 ± 0.4	<0.1
June 4, 1968	0.2 ± 0.1	<0.1
August 9, 1968	3.2 ± 1.5	<0.1

(5 per tube) were planted at each of three depths—20, 40, and 60 mm. Twenty-two days after planting, we cut the tubes and washed the soil from the seedlings and non-germinated seeds. Morphological features were measured; and representative plants were photographed.

Results

The plow, pack and drill system produced good stands of crested wheatgrass in 8 of 9 trials (Table 1). Seeds planted June 4, 1968, produced a poor stand because of a heavy hailstorm the day after planting. On the other hand, blue grama was never successful, even though it emerged quickly and produced initially thick stands in most trials. In each case, blue grama died at an age of 6 to 10 weeks.

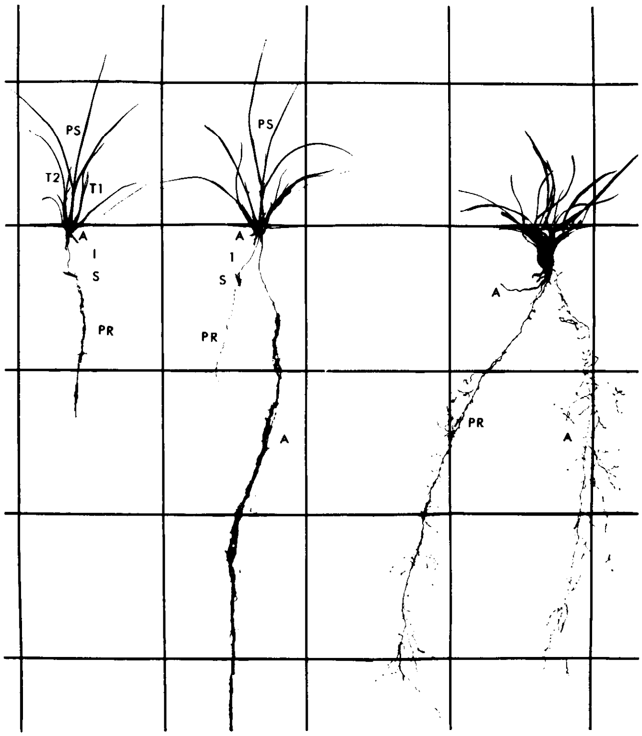

Fig. 2. Grass seedlings 6 weeks after planting in the field. Mounted on a 5 cm grid. Left: blue grama with primary root deteriorating and adventitious roots only dead stubs. Center: blue grama with one long adventitious root and others dead. Right: crested wheatgrass with active primary and adventitious roots. S = seed, PR = primary root, A = adventitious root, I = first or sub-coleoptile internode, PS = primary shoot, T1 = tiller number 1, T2 = tiller number 2.

Table 2. Morphological features of blue grama and crested wheatgrass seedlings 22 days after planting in the greenhouse (measurements include mean and standard deviation).

Species and item	Seedlings emerged from:			Seedlings not emerged from:		
	20 mm	40 mm	60 mm	20 mm	40 mm	60 mm
Blue grama:						
Percent germinated	80	35	0	0	25	75
Coleoptile length, mm	6 ± 1	7 ± 2	–	–	7 ± 2	7 ± 2
Sub-coleoptile internode length, mm	18 ± 2	30 ± 2	–	–	22 ± 10	23 ± 12
Primary root length, mm	81 ± 30	41 ± 20	–	–	16 ± 7	18 ± 6
Number of lateral roots	0	0	–	–	0	0
Number of adventitious roots	0.5	0.7	–	–	0	0
Total length of adventitious roots, mm	14	10	–	–	0	0
Depth to adventitious roots, mm	2 to 6	7 to 10	–	–	–	–
Plumule length, mm	79 ± 32	59 ± 51	–	–	10 ± 2	11 ± 6
Crested wheatgrass:						
Percent germinated	50	70	20	5	10	80
Coleoptile length, mm	24 ± 3	34 ± 6	44 ± 9	10	12	29 ± 6
Intra-coleoptile internode length, mm	0	6 ± 6	12 ± 15	0	0	0
Primary root length, mm	96 ± 47	99 ± 47	72 ± 39	60	35	28 ± 15
Number of lateral roots	1.2	1.4	0.5	0	0.5	0
Total length of lateral roots, mm	44	42	5	0	5	0
Number of adventitious roots	0	0.6	0.8	0	0	0
Depth to adventitious roots, mm	20	34 to 40	48 to 60	–	–	–
Plumule length, mm	148 ± 88	188 ± 88	138 ± 45	10	20	67 ± 25

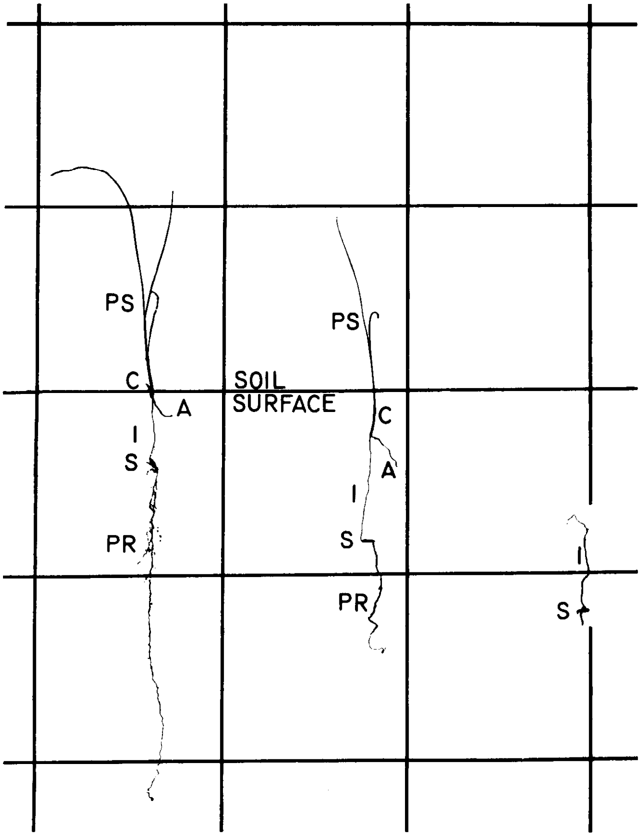

Fig. 3. Blue grama seedlings grown in the greenhouse from seeds planted 20, 40 and 60 mm deep (left to right). Plants are mounted on a 5 cm grid. PS = primary shoot, C = coleoptile, I = sub-coleoptile internode, S = seed, PR = primary root, A = adventitious root.

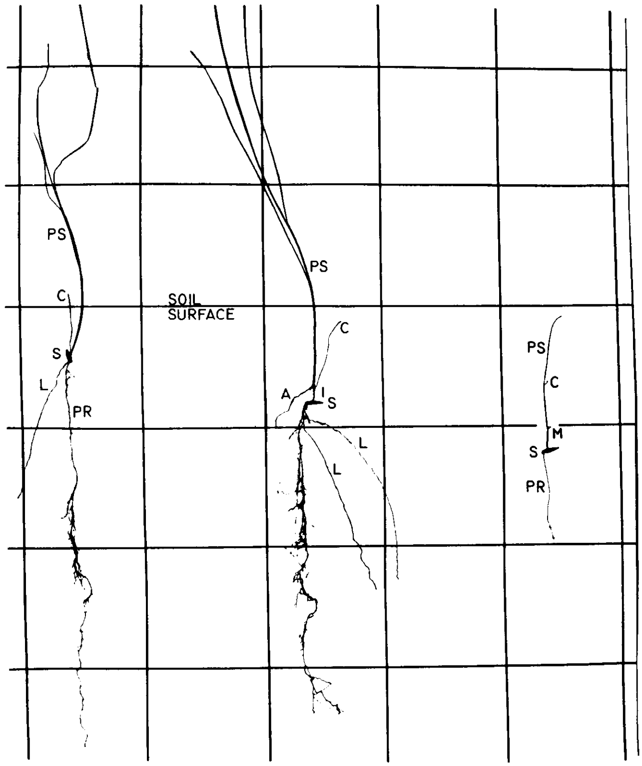

Fig. 4. Crested wheatgrass seedlings grown in the greenhouse from seeds planted 20, 40 and 60 mm deep (left to right). Plants are mounted on a 5 cm grid. PS = primary shoot, L = lateral root, A = adventitious root, M = leaf meristem loop (see text), I = intra-coleoptile internode.

Blue grama, which has a panicoid-type morphology, had a single seminal root (the primary root) which seldom grew longer than 10 cm. These primary roots began deteriorating at 5 to 6 weeks of age. In the process of emergence, the coleoptile and enclosed shoot were elevated to the soil surface by elongation in the sub-coleoptile internode (Fig. 2). This elongation placed the origin of adventitious roots within 6 mm of the soil surface. At this depth the soil is dry except during or immediately after a rain. Adventitious roots were nearly always dead stubs. Most plants reached the two-tiller stage of development on the primary root alone. A few plants had a single, long adventitious root, as did the center plant in Figure 2.

Crested wheatgrass, which has a festucoid-type morphology, developed a seminal primary root, an occasional seminal lateral root (maximum of 5) and adventitious roots—all arising at or near the depth of planting (plant on right in Figure 2). There was no elongation in the sub-coleoptile internode. Even though most plants developed a good adventitious root, they always had many dead root stubs. The small number of surviving adventitious roots on crested wheatgrass probably accounts for the very slow growth of its seedlings. Two factors account for better survival of crested wheatgrass than of blue grama; namely, crested wheatgrass has (1) a longer lived primary root and (2) a deeper origin of adventitious roots.

Comparative lengths of various structures of blue grama and crested wheatgrass seedlings grown in the greenhouse are shown in Table 2. Representative plants from seed planted at depths of 20, 40, and 60 mm are shown in Figures 3 and 4.

When planted at 20 mm, blue grama always emerged if germination occurred. The coleoptile averaged 6 mm long and the sub-coleoptile internode averaged 18 mm. Thus, the total length of emergence structures was 24 mm, which places the coleoptilar node (and depth of origin of adventitious roots) just 2 mm below the surface. When planted at 40 mm, slightly more than half the seedlings emerged. However, the total average length of coleoptile and sub-coleoptile internode was 37 mm. If coleoptiles fail to reach the soil surface, plant emergence is unlikely. Blue grama seedlings failing to emerge from 40 and 60 mm had sub-coleoptile internode lengths near 23 mm and coleoptile lengths of 7 mm; consequently, the maximum planting depth is 30 mm. This total length is the reach of the coleoptile. To obtain best emergence and seedling development, the optimum planting depth is 15 to 20 mm. Since the coleoptile length is nearly constant and adventitious roots arise from the coleoptilar and subsequent nodes, planting depth does not materially affect the depth of adventitious rooting. The death of adventitious roots originating so near the surface is a problem that must be solved in some way other than by depth of planting; that is, by mulching or by irrigation.

A few comments regarding the most satisfactory types of mulch for blue grama are needed. The main point is that the mulch utilized must not cause even greater elevations of the coleoptilar nodes, which are the sites of adventitious rooting. When blue grama seeds were planted 1 cm deep in soil covered with 3 cm of sawdust, the coleoptilar nodes were elevated above the soil surface into the sawdust 1 to 1.5 cm. Sawdust removal 2 weeks after seedling emergence left the plumules hanging by sub-coleoptile internodes and adventitious roots. Consequently, a thick, opaque type of mulch (such as sawdust, sand, or soil) is unsatisfactory unless it can be applied after seedling emergence (without covering the leaves) when the level of adventitious rooting by the seedling is fixed. Rather than applying thick, opaque mulches after emergence, one could apply a thin moisture barrier such as an asphalt emulsion mulch (Bement, et al., 1961) or an open (transparent) straw or stubble mulch (Fults, 1944; Glendening, 1942; Savage, 1939). These types of mulching materials are adaptable to blue grama, and probably could be used to improve its establishment. At this time we do not attempt to evaluate the various types of mulch in terms of their effectiveness for retaining a moist soil surface.

When planted at 20 mm, crested wheatgrass had a coleoptile length of 24 mm. When planted at 40 and 60 mm, coleoptile lengths averaged 34 and 44 mm, respectively. If the coleoptile does not reach the soil surface, emergence is unlikely when the soil offers much resistance to the leaf as it grows out of the coleoptile. The leaf is poorly adapted to emergence because it has a long, soft meristematic region at its base inside the coleoptile. When the exserted leaf blade meets resistance, the meristematic tissue kinks and eventually forms a loop that breaks through the wall of the coleoptile, as shown at "M" with the plant on the right in Figue 4. This meristematic loop was common on plants that failed to emerge. Because of these growth characteristics, the proper depth for planting crested wheatgrass is 20 to 30 mm. Within this range of planting depths, the maximum can be used in light-textured, sandy soils and the minimum in heavy-textured soils. Deeper planting increases the depth of adventitious rooting; however, intra-coleoptile internode elongation elevates the origin of some adventitious roots a little above planting depth, as shown by the center plant in Figure 4. Sawdust, or other opaque-type mulches, would be suitable for crested wheatgrass provided that the total depth of seed coverage will permit seedling emergence.

Conclusion

A blue grama seedling has a short coleoptile (6 mm), which can not independently emerge from a seeding depth greater than 7 mm. However, the coleoptile and enclosed shoot are elevated to the soil surface by elongation of the sub-coleoptile internode situated below the divergence of the coleoptile. This elongation places the origin of adventitious roots at a soil depth of 6 mm or less (average only 2 mm). At that depth, conditions usually are unfavorable for continued growth. On the Shortgrass Plains of Colorado, blue grama seedlings generally die 6 to 10 weeks after seeding because the adventitious roots do not grow out of the dry soil near the surface. Crested wheatgrass has a long coleoptile (readily up to 3 cm) and no elongation in the sub-coleoptile internode. This morphology places the adventitious roots (originating from the coleoptilar node) at the depth of seeding. In addition, adventitious roots may arise at slightly higher positions, if the intra-coleoptile internode, situated above the divergence of and inside the coleoptile, elongates. Since growing conditions for adventitious roots are more favorable at planting depth (about 20 mm) than at 2 mm below the surface, crested wheatgrass is more likely to survive than is blue grama.

Literature Cited

Bement, R. E., D. F. Hervey, A. C. Everson, and L. O. Hylton, Jr. 1961. Use of asphalt-emulsion mulches to hasten grass-seedling establishment. J. Range Manage. 14:102–109.

Boatwright, G. O., and Hayden Ferguson. 1967. Influence of primary and/or adventitious root systems on wheat production and nutrient uptake. Agron. J. 59:299–302.

Boyd, Lucy, and George S. Avery, Jr. 1936. Grass seedling anatomy: The first internode of *Avena* and *Triticum*. Bot. Gaz. 97:765–779.

Esau, Katherine. 1960. Anatomy of seed plants. John Wiley and Sons, Inc., New York. 170 p.

Fults, J. L. 1944. Some factors affecting the establishment of perennial grass for erosion control in eastern Colorado. J. Am. Soc. Agron. 36:615–625.

Glendening, G. E. 1942. Germination and emergence of some native grasses in relation to litter cover and soil moisture. J. Am. Soc. Agron. 34:797–804.

GP-6 Technical Committee. 1966. A stand establishment survey of grass plantings in the Great Plains. Great Plains Council Report No. 23, Nebr. Agr. Exp. Sta., 60 p.

Hyder, D. N., and R. E. Bement. 1969. A micro-ridge roller for seedbed modification. J. Range Manage. 22: 54–56.

HYDER, D. N., AND R. E. BEMENT. 1970. Soil physical conditions after plowing and packing of ridges. J. Range Manage. 23:289–292.

MARLATT, W. E., AND D. N. HYDER. 1970. Soil ridging for reduction of wind erosion from grass seedbeds. J. Range Manage. 23:169–173.

MCGINNIES, W. J., D. F. HERVEY, J. A. DOWNS, AND A. C. EVERSON. 1963. A summary of range grass seeding trials in Colorado. Colo. Agr. Exp. Sta. Tech. Bull. 73, 81 p.

RIEGEL, ANDREW. 1941. Life history and habits of blue grama. Transactions. Kans. Acad. Sci. 44:76–83.

SARGANT, ETHEL, AND AGNES ARBER. 1915. The comparative morphology of the embryo and seedling in the *Gramineae*. Annals of Bot. 24:161–222.

SAVAGE, D. A. 1939. Grass culture and range improvement in the Central and Southern Great Plains. U. S. Dep. Agr. Circ. 491.

TAYLOR, J. W., AND M. A. MCCALL. 1936. Influence of temperature and other factors on the morphology of the wheat seedling. J. Agr. Res. 52:557–568.

WEAVER, J. E., AND ELLEN ZINK. 1945. Extent and longevity of the seminal roots of certain grasses. Plant Physiol. 20: 359–379.