Drought Tolerance of Seminal Lateral Root Apices in Crested Wheatgrass and Russian Wildrye

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Highlight: Germinating seed of crested wheatgrass (*Agropyron desertorum*) and Russian wildrye (*Elymus junceus*) were exposed to temporary drought, and the capacity for development of seminal lateral roots was then determined under conditions of favorable soil moisture. After a temporary drought of −370, −910, and −1580 bars, 75, 58, and 24% of the crested wheatgrass seedlings and 69, 20, and 6% of the Russian wildrye seedlings developed seminal lateral roots, respectively. Because actively growing seminal primary roots may be killed by temporary drought and because germinating seed and young seedlings lack the capacity for development of adventitious roots, the growth and survival of seedlings often may depend on the development of seminal lateral roots.

In semiarid regions, there is often no alternative but to plant during seasons when germinating seed will be exposed to drought. Under these conditions, emergence and establishment may depend on the tolerance of germinating seed to temporary drought and on their capacity for recovery during subsequent periods of favorable moisture. The capacity for root development after temporary drought is especially critical in the early growth and survival of seedlings.

The seminal primary root, which develops from the lower end of the embryo, is the first root of a grass seedling. In certain species of the Festucoideae subfamily, including crested wheatgrass (*Agropyron desertorum*) and Russian wildrye (*Elymus junceus*), the next roots that develop are the seminal lateral roots. Seminal lateral roots develop from primordia at the scutellar node (Boyd and Avery 1936; Hyder 1974). However, many grass species entirely lack the potential for seminal lateral root development (Hoshikawa 1969). At later stages of grass seedling growth, adventitious roots may arise from the coleoptilar and higher nodes of the main shoot, from nodes of tillers, and in certain species from the subcoleoptile internode (Hoshikawa 1969; Hyder 1974).

Survival drought tolerance is defined as the capacity of plants or of germinating seed to endure the dehydration of their tissues (Levitt 1964), and it is quantified from relationships between degree of plant drought (i.e., water potential of plant tissues) and percentage death. Drought tolerance is related to the capacity of cells, membranes, cytoplasm, and organelles to endure dehydration without experiencing destructive structural and chemical changes (Toole et al. 1956; Wilson et al. 1970; Maguire 1972; Wilson 1973).

This study was conducted to evaluate the responses of germinating seed of 'Nordan' crested wheatgrass and 'Vinall' Russian wildrye to temporary drought. These responses were evaluated by determining total germination, rate of germination, length of shoots, and length of roots in a growth performance test under favorable moisture conditions. The objectives were to define the role of seminal lateral roots in the survival of germinating seed after exposure to drought, to determine the latent potential for seminal lateral root deveopment, and to quantify the drought tolerance of shoot apices and seminal lateral root apices. These species were selected because of evidence that germinating seed of crested wheatgrass are less susceptible to drought injury than those of Russian wildrye (Bleak and Keller 1974).

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Materials and Methods

Seed Sources and Experimental Treatments

Seed of crested wheatgrass (produced in North Dakota in 1973) and of Russian wildrye (produced in Montana in 1974) were cleaned in an air column to remove inert material and light-weight seed. Germination tests at 10°C indicated 91% germination for crested wheatgrass and 94% germination for Russian wildrye. In these tests, crested wheatgrass and Russian wildrye reached 50% germination in 10 days and 12 days, respectively. Seed were treated with 15 mg of thiram, bis (dimethylthiocarbamoyl) disulfide, per gram dry weight of seed to minimize microbiological contamination.

The experimental procedures included three consecutive steps: (1) a wet treatment to initiate seed germination, (2) a temporary drought treatment, and (3) a germination or growth performance test to determine the effects of the temporary drought treatment. The research included two experiments. The first dealt with the role of seminal lateral roots under drought conditions, and the second dealt with the drought tolerance of seminal lateral root apices. The methods used in the two experiments are given under separate subheadings.

Role of Seminal Lateral Roots under Drought Conditions

During the initial wet treatment, samples of 200 seed were placed on moist blotter paper in dishes and kept in darkness in a germinator set for 10°C. We observed dishes at 12-hour intervals and removed germinating seed when the seminal primary root had extended to a length of 2 to 5 mm. One hundred twenty-five germinating seed were removed from each dish and were air-dried for 4 to 6 days at 23°C in open dishes in the laboratory. Most of the germinating seed had not developed a visible coleoptile when they were removed from the dishes.

Responses of germinating seed to temporary drought were evaluated in a 30-day germination test. Samples of 100 treated or untreated seed were placed on moist blotter paper in germination dishes, and dishes were kept in darkness in a germinator at 10°C. This temperature was selected because it is typical of average soil temperatures at planting depth in the spring and fall (Wilson et al. 1974). In related studies, constant temperatures in a germinator and variable temperatures in the field influenced the germination of crested wheatgrass seed in a similar way (Wilson 1973). The number of seedlings with a living root, a living shoot, or both, were counted daily. High turgidity was a characteristic used for identification of living shoots or roots. The presence of root hairs was also a reliable indicator of a living root.

The effects of temporary drought on germinating seed were also evaluated in a 20-day growth performance test. Samples of 25 treated or untreated seed were planted at a depth of 2 cm in plastic pots (15 cm diameter by 15 cm deep) filled with autoclaved sandy loam soil. Pots were placed in a growth chamber set for 10°C and a daylength of 12 hours. Maximum photosynthetic flux density attainable in the growth chamber used in this experiment was about 160 microeinsteins/m^2 per sec. Soil was maintained near field capacity by irrigating with distilled water two or three times weekly. At 20 days, all pots were removed from the growth chamber, soil was washed from the roots, and shoot and root lengths were measured. Roots did not extend to the bottom of the pots in the 20-day test. Thus, pots were large enough not to restrict root growth.

Drought Tolerance of Seminal Lateral Root Apices

The initial wet treatment was accomplished as described in the first experiment. We removed seed from dishes when the seminal primary root had extended to a length of 2 to 5 mm. Seed that had not yet developed a visible shoot were selected for exposure to temporary drought. We excised the entire seminal primary root with a scalpel and dried the seed for 4 days at constant water potentials. The seminal primary root was excised so that root development during the growth performance test would depend entirely on the capacity for seminal lateral roots. Water potentials of −100, −220, −370, −910, or −1580 bars were maintained over saturated solutions of Na_2SO_4, KCl, NaCl, $Ca(NO_3)_2$, and $CaCl_2$, respectively (Spencer 1926; Wilson and Harris 1968). These water potentials are typical of those found in soil on semiarid lands (Wilson et al. 1970; Wilson 1973). After treatment at constant water potentials, seed were dried at 70°C for 24 hours to determine water percentage on a fresh weight basis.

The effects of temporary drought on germinating seed were determined in the 20-day growth performance test at 10°C. Untreated seed from air-dry storage and germinating seed (seminal primary root excised) that had not been exposed to drought were included in the test to determine the latent potential for development of seminal lateral roots. Seedlings were grown in a growth chamber where the photosynthetic photon flux density was 480 microeinsteins/m^2 per sec.

Experimental Design and Statistical Procedures

Each value for percentage germination is based on a sample of 100 seed in a dish. In the growth performance tests, each value for percentage of seedlings with a shoot or root, average length of shoot or root, and average number of roots per seedling is based on a sample of 25 seed planted in a pot filled with soil. Length of shoot is the distance from the seed to the tip of the longest leaf and is based on the number of seedlings that developed a shoot. Length of root is the total length of the main axis of all seminal roots. Values for average length of root and average number of roots per seedling are based on the number of seedlings that developed a root.

A randomized complete block experimental design was used for both experiments. The first experiment included eight replications, and the second experiment included 16 replications. Analysis of variance and Duncan's multiple range test were used for determining significant differences among treatment means. Differences among treatments and between species noted in the text are significant at either the 0.05 or 0.01 level.

Results

Role of Seminal Lateral Roots in Drought Conditions

Seed water content at the end of the air-dry treatment was 8%. Seminal primary roots, which had extended to a length of 2 to 5 mm during the initial wet treatment, were killed by the temporary drought treatment.

In the germination test of untreated seed of crested wheatgrass (Fig. 1A) and Russian wildrye (Fig. 2A), growth of seminal primary roots preceded growth of the shoot by about 2 days. However, in the germination test of treated crested wheatgrass, development of shoots preceded the development of seminal lateral roots by about 8 days (Fig. 1B). By the end of the 30-day germination test, 40% of treated crested wheatgrass seed had developed a shoot and 26% had developed one or more seminal lateral roots. In contrast, a maximum of 7% of the treated Russian wildrye seed developed a shoot and none of the treated seed developed a seminal lateral root (Fig. 2B). Some shoots that were not supported by a root died during the 30-day germination test which accounts for the occasional decreases in the number of treated seed with a living shoot (Figs. 1B and 2B).

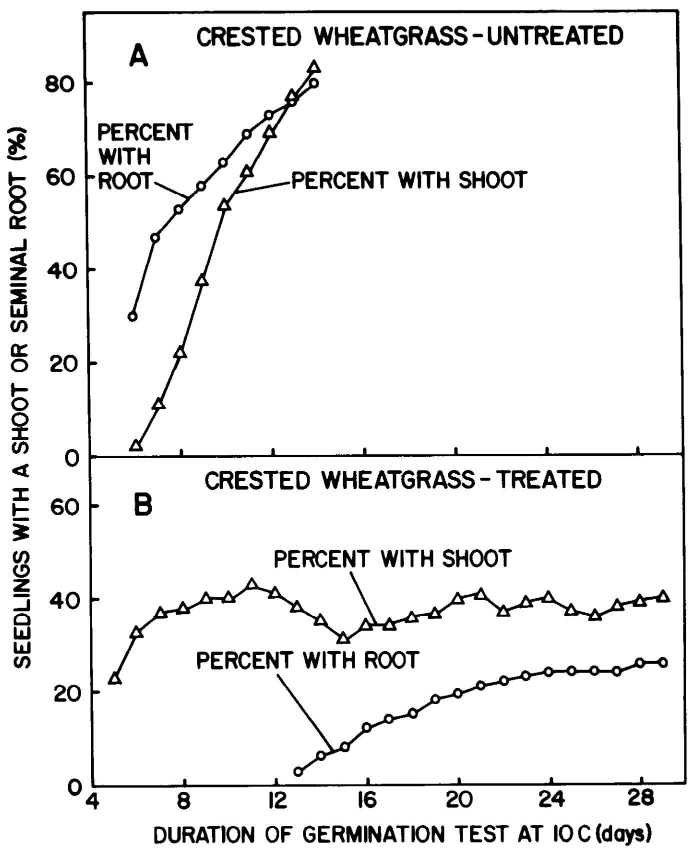


Fig. 1. *Shoot and root development for treated and untreated crested wheatgrass in a germination test of 10°C.*

In the 20-day growth test, which was conducted to evaluate the effects of temporary drought, the percentages of germinating seed that developed a shoot indicated the susceptibility of either shoot apices or coleoptiles, or both, to drought injury. Percentages of seedlings that had developed a shoot at 20 days were 62 and 90 for treated and untreated crested wheatgrass and 21 and 94 for treated and untreated Russian wildrye, respectively (Table 1). The first and second leaves extended from coleoptiles that emerged during the growth performance test.

Table 1. Effects of air-drying germinating seed of crested wheatgrass and Russian wildrye (when the seminal primary root was 2 to 5 mm long) on the percentage that developed a shoot or root and on average length of shoot or root (cm) produced in a 20-day growth performance test at 10°C.

Growth criteria and species	Untreated seed[1]	Treated seed[2]	Mean
% with a shoot			
Crested wheatgrass	90 c[3]	62 b	76 z
Russian wildrye	94 c	21 a	58 y
% with a root			
Crested wheatgrass	82 c	42 b	62 z
Russian wildrye	88 c	4 a	46 y
Average length of shoot			
Crested wheatgrass	4.9	3.5	4.2 z
Russian wildrye	3.7	2.4	3.0 y
Treatment mean	4.3 b	3.0 a	
Average length of root			
Crested wheatgrass	3.3	1.4	2.4 z
Russian wildrye	2.3	0.4	1.4 y
Treatment mean	2.8 b	0.9 a	

[1] Untreated seed produced a seminal primary root and occasionally a seminal lateral root.
[2] Because all seminal primary roots were killed by the temporary drought treatment, root data are for seminal lateral roots.
[3] Means within each criterion of growth performance labeled with the same letter are not significantly different at the 0.05 level. Because there was not a significant interaction for length of shoot and length of root, statistical differences are shown only for the main effects (species and treatments). Each value represents the mean of 8 pots with 25 seed planted per pot.

Thus, both the coleoptile and the shoot apex were drought tolerant in these seedlings.

Untreated seed developed a seminal primary root and occasionally a seminal lateral root during the 20-day growth performance test. However, they did not develop adventitious roots. Because all seminal primary roots in treated seed had been killed by temporary drought and because seedlings did not develop adventitious roots, root development during the 20-day test depended entirely on the capacity for development of seminal lateral roots. At 20 days, the percentages with a root were 42 and 82% for treated and untreated crested wheatgrass and 4 and 88% for treated and untreated Russian wildrye, respectively (Table 1). The analysis of variance indicated a significant interaction between treatments and species in relation to development of seminal roots. The temporary drought treatment reduced average lengths of both shoots and roots (Table 1).

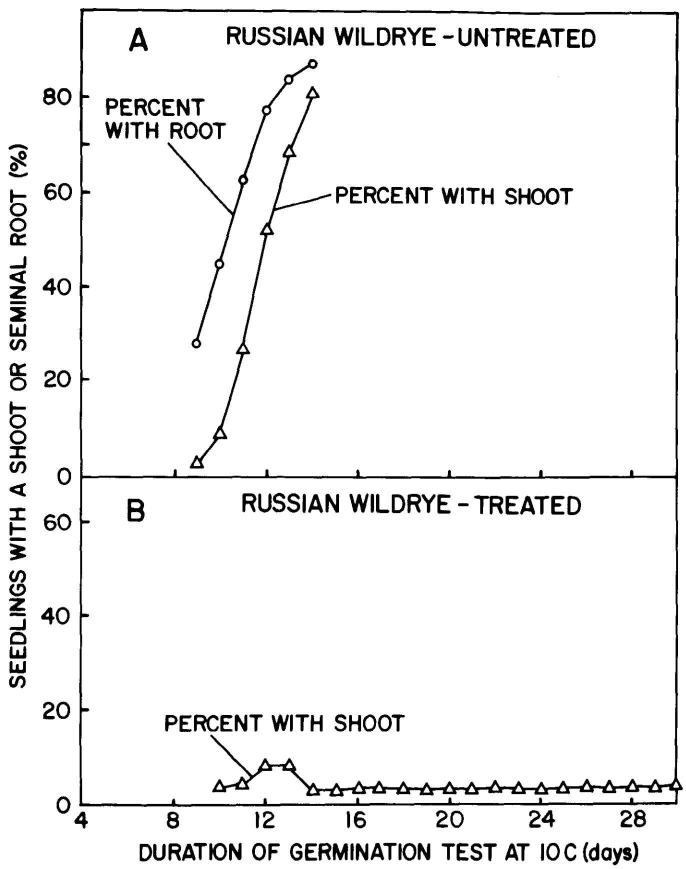


Fig. 2. *Shoot and root development for treated and untreated Russian wildrye in a germination test at 10°C.*

Drought Tolerance of Seminal Lateral Root Apices

The time course of water loss from germinating seed during temporary drought in constant humidity environments is given in Table 2. Crested wheatgrass and Russian wildrye did not differ in capacity for water uptake during the initial wet treatment or in resistance to water loss during exposure to temporary drought. At the end of the 4-day drought treatment, seed water content ranged from 23.9% at −100 bars to 7.8% at −1580 bars.

Table 2. Water content (%) of seed of crested wheatgrass and Russian wildrye after 0, 1, 2, 3, or 4 days of drought treatment at various water potentials.

Days of exposure to temporary drought	Water potentials (bars)[1] −100	−220	−370	−910	−1580
0 days					
Crested wheatgrass	45.9	46.2	47.2	46.2	46.2
Russian wildrye	45.8	46.6	46.0	45.5	46.0
Mean	45.9i[2]	46.4i	46.6i	45.8i	46.1i
1 day					
Crested wheatgrass	27.8	19.0	15.6	12.5	8.8
Russian wildrye	27.9	20.4	16.5	14.1	9.0
Mean	27.9h	19.7f	16.0e	13.3d	8.9b
2 days					
Crested wheatgrass	24.5	16.5	13.8	11.2	7.6
Russian wildrye	24.8	16.9	14.0	11.9	7.6
Mean	24.7g	16.7e	13.9d	11.6c	7.6a
3 days					
Crested wheatgrass	24.7	16.4	13.9	10.9	7.4
Russian wildrye	23.9	16.3	13.7	11.4	7.1
Mean	24.3g	16.4e	13.8d	11.2c	7.2a
4 days					
Crested wheatgrass	23.5	16.3	13.9	10.8	7.8
Russian wildrye	24.2	16.3	13.9	11.6	7.7
Mean	23.9g	16.3e	13.9d	11.2c	7.8a

[1] Drought treatments were imposed after seed had absorbed water from moist blotter paper for 2 days at 10°C.
[2] Treatment means labeled with the same letter are not significantly different at the 0.05 level of probability.

When seminal primary roots were excised and the germinating seed planted in moist soil without exposure to temporary drought, the percentages of crested wheatgrass and Russian wildrye seed that developed a seminal lateral root were 83 and 86, respectively (Table 3). Average total length of seminal lateral roots was 6.5 cm for crested wheatgrass and 5.0 cm for Russian wildrye. The average number of seminal lateral roots was 1.6 for both crested wheatgrass and Russian wildrye.

Exposure of germinating seed to a temporary drought of −100, −220, or −370 bars had little injurious effect on the percentages of crested wheatgrass and Russian wildrye seedlings that developed a shoot during the 20-day growth performance test (Fig. 3). However, water potentials of −910 and −1580 bars significantly reduced the percentages that developed a shoot.

Water potentials of −910 and −1580 bars for crested wheat-

Table 3. **Latent potential for seminal lateral roots in germinating seed of crested wheatgrass and Russian wildrye as indicated by percentage of seedlings with a root, average length of roots (cm), and average number of roots per seedling produced in a 20-day test at 10°C.**

Growth criteria and species	Untreated seed[1]	Seminal primary root excised[2]	Mean
% with a root			
Crested wheatgrass	87	83	85 y[3]
Russian wildrye	94	86	90 z
Treatment mean	90 b	84 a	
Average length of root			
Crested wheatgrass	5.0	6.5	5.8 z
Russian wildrye	3.3	5.0	4.1 y
Treatment mean	4.2 a	5.7 b	
Average number of roots			
Crested wheatgrass	1.2	1.6	1.4 y
Russian wildrye	1.0	1.6	1.3 y
Treatment mean	1.1 a	1.6 b	

[1] Untreated seed from air-dry storage produced a seminal primary root and occasionally a seminal lateral root. Adventitious roots did not develop during the 20-day test.
[2] Seminal primary roots were excised when they had extended to a length of 2 to 5 mm. Therefore, all root values in this treatment are for seminal lateral roots.
[3] Species or treatment means (within each criterion of growth performance) labeled with the same letter are not significantly different at the 0.05 level of probability. Each value represents the mean of 16 pots with 25 seed planted per pot.

grass and −370, −910, and −1580 bars for Russian wildrye significantly reduced the percentage of seedlings that developed a seminal lateral root (Fig. 3). After a temporary drought of −370, −910, and −1580 bars, 75, 58, and 24% of the crested wheatgrass seedlings and 69, 20, and 6% of the Russian wildrye seedlings developed seminal lateral roots, respectively.

Only a water potential of −1580 bars reduced average shoot lengths of crested wheatgrass, but all water potential treatments reduced average shoot lengths of Russian wildrye (Fig. 4).

Average total length of seminal lateral roots per seedling decreased in both species and in all drought treatments except

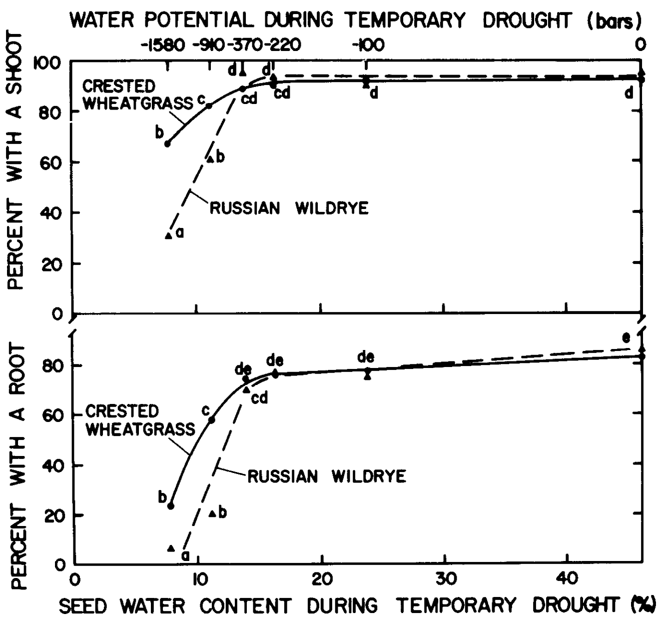


Fig. 3. *Effects of various degrees of temporary drought on the percentage of crested wheatgrass and Russian wildrye seedlings that developed a shoot or a seminal lateral root during a 20-day growth performance test at 10°C. Water potentials indicate the temporary drought treatment that corresponds to the measured water content.*

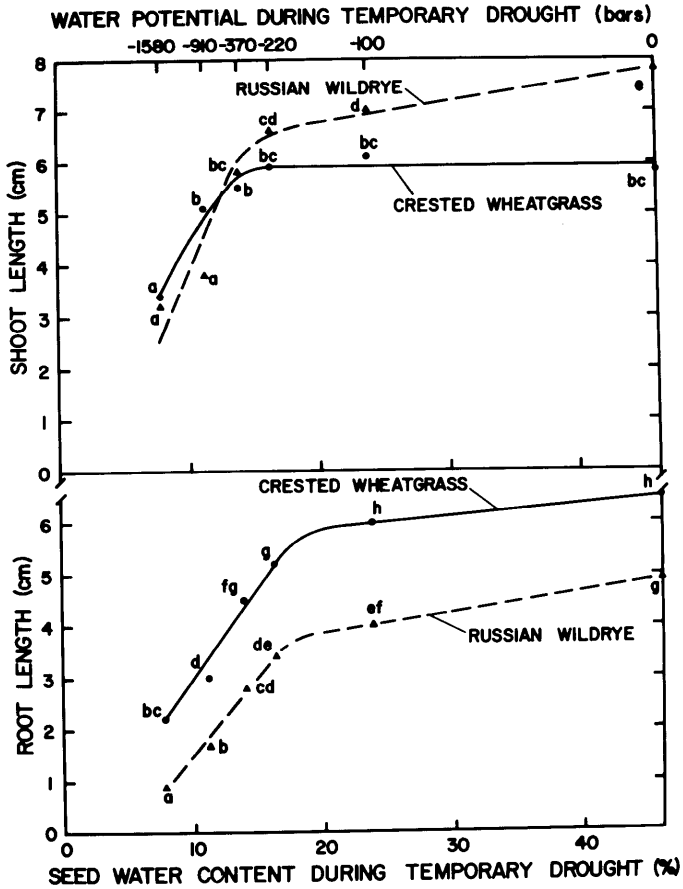


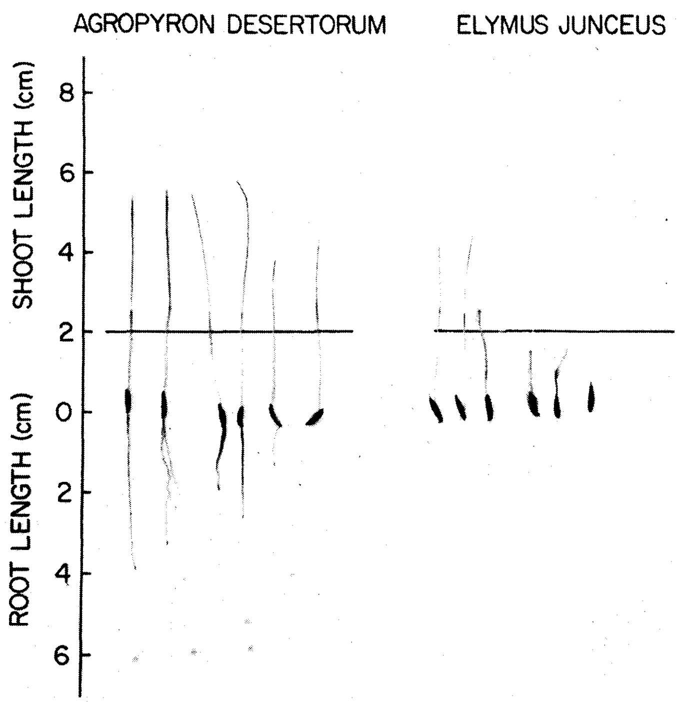
Fig. 4. *Effects of various degrees of temporary drought on average length of shoot and seminal lateral root produced during a 20-day growth performance test at 10°C. Water potentials indicate the temporary drought treatment that corresponds to the measured water content.*

−100 bars for crested wheatgrass (Figs. 4 and 5). At −370, −910, and −1580 bars, average root lengths were 4.5, 3.0, and 2.2 cm for crested wheatgrass and 3.0, 1.7, and 0.9 cm for Russian wildrye. Thus, temporary drought inhibited root development more than shoot development and injured Russian wildrye more than crested wheatgrass.

Discussion

Drought tolerance is related in part to embryo morphology during seed development and germination. In particular, it is influenced by the presence or absence of root primordia at the scutellar note of the mature grass embryo (Boyd and Avery 1936) and by tne capacity for root development from these primordia.

In germinating seed of crested wheatgrass and Russian wildrye, the seminal primary root develops first. Seminal lateral root primordia at the scutellar note remain quiescent for several days or weeks after planting and then develop sequentially, one or two at a time. In this quiescent condition, they are less susceptible to drought injury than the apex of the actively growing seminal primary root. Thus, when the seminal primary root is killed by temporary drought, the subsequent development of one or more seminal lateral roots provides the seedling with a replacement source of water and nutrients. In this study, germinating seed and young seedlings of crested wheatgrass and Russian wildrye lacked capacity for development of adventitious roots.



TEMPORARY DROUGHT: 31% RH

Fig. 5. *Examples of seminal lateral root development in crested wheatgrass (*A. desertorum*) and absence of seminal lateral root development in Russian wildrye (*E. junceus*) during a 20-day growth performance test at 10°C. The entire seminal primary root was excised when it had extended to a length of 2 to 5 mm. Germinating seed were exposed to a drought of −1580 bars (31% relative humidity) for 4 days and then planted in moist soil for the growth performance test. The examples represent the six best seedlings from one replication.*

Seed of crested wheatgrass and Russian wildrye did not differ in resistance to water loss during temporary drought. Undried seed (seminal root excised) of the two species did not differ in percentage of seedlings that developed seminal lateral roots or in average numbers of roots per seedling. However, crested wheatgrass was superior to Russian wildrye in total length of seminal lateral roots (Table 3). Therefore, differences between species in seminal lateral root development, after exposure to temporary drought, were apparently due to differences in latent potential for growth of seminal lateral roots as well as differences in drought tolerance of seminal lateral root apices.

Bleak and Keller (1974), working with six range grasses, encountered no significant negative effects of preplanting seed treatment, with the possible exception of the behavior of Russian wildrye. In their study, seed were retained in a moist environment until approximately 5% had developed visible roots. Seed were then spread out and air-dried. This pretreatment improved the early emergence of seedlings in field plantings for all species except Russian wildrye. Our results help explain why preplanting treatment of Russian wildrye was not as effective in promoting early emergence as preplanting treatment of crested wheatgrass.

The water potentials investigated in this study were comparable to those of surface soil in field plantings during the spring and fall (Wilson et al. 1970). These investigators found that soil moisture conditions were more favorable at a depth of 2.5 cm than at the soil surface. Thus in some situations, drought injury may be reduced by increasing the depth of planting; however, emergence of crested wheatgrass and Russian wildrye may be adversely affected when planting depth is greater than 2.5 cm (McGinnies 1973).

Variability within species in capacity for seminal lateral root development after temporary drought suggests the opportunity to select for this drought tolerance adaptation. Cultivars with improved drought tolerance should reduce planting failures. Species and cultivars that possess low drought tolerance of root apices, or exhibit a low inherent capacity for seminal lateral root development, or entirely lack seminal lateral roots, are most susceptible to drought injury and least suited for planting on semiarid lands.

Literature Cited

Bleak, A. T., and W. Keller. 1974. Emergence and yield of six range grasses planted on four dates using natural and treated seed. J. Range Manage. 27:225-227.

Boyd, L., and G. S. Avery, Jr. 1936. Grass seedling anatomy: the first internode of *Avena* and *Triticum*. Bot. Gaz. 97:765-779.

Hoshikawa, K. 1969. Underground organs of the seedlings and the systematics of the gramineae. Bot. Gaz. 130:192-203.

Hyder, D. N. 1974. Morphogenesis and management of perennial grasses in the United States, p. 89-98. *In:* Proceedings of the Workshop of the United States-Australia Rangelands Panel, Berkeley, California, March 29-April 5, 1971. U.S. Dep. Agr. Misc. Pub. No. 1271.

Levitt, J. 1964. Drought, p. 57-66. *In:* Forage plant physiology and soil-range relationships. Amer. Soc. Agron. Special Pub. No. 5.

Maguire, J. D. 1972. Physiological disorders in germinating seeds induced by the environment, p. 289-310. *In:* W. Heydecker (ed.) Seed Ecology. The Pennsylvania State Univ. Press, University Park.

McGinnies, W. J. 1973. Effects of date and depth of planting on the establishment of three range grasses. Agron. J. 65:120-123.

Spencer, H. M. 1926. Laboratory methods for maintaining constant humidity, p. 67-68. *In:* E. W. Washburn (ed.) International Critical Table, Vol. 1. McGraw Hill Book Co., Inc., New York.

Toole, E. H., S. B. Hendricks, H. A. Borthwick, and V. K. Toole. 1956. Physiology of seed germination. Annu. Rev. Plant Physiol. 7:299-324.

Wilson, A. M., and G. A. Harris. 1968. Phosphorylation in crested wheatgrass at low water potentials. Plant Physiol. 43:61-65.

Wilson, A. M., J. R. Nelson, and C. J. Goebel. 1970. Effects of environment on the metabolism and germination of crested wheatgrass seeds. J. Range Manage. 23:283-288.

Wilson, A. M. 1973. Responses of crested wheatgrass seeds to environment. J. Range Manage. 26:43-46.

Wilson, A. M., D. E. Wondercheck, and C. J. Goebel. 1974. Responses of range grass seeds to winter environments. J. Range Manage. 27:120-122.