Root morphological development in relation to shoot growth in seedlings of four range grasses

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Abstract

Successful seedling establishment in arid and semiarid rangelands depends on seedling root characteristics and on the relationship between shoot and root development. This study was conducted to determine seedling shoot and root developmental characteristics of 'Hycrest', a hybrid cultivar of crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult. × Agropyron cristatum (L.) Gaert.]; 'Whitmar', a cultivar of bluebunch wheatgrass [Pseudoroegneria spicata (Pursh) Love subspecies inermis (Scrib. and Smith) Löve]; 'Secar', a cultivar of Snake River wheatgrass [Elymus lanceolatus (Scribner & J.G. Smith) Gould]; and cheatgrass (Bromus tectorum L.) under favorable growth conditions. Seedlings were grown in 20-cm × 20-cm pots filled with sandy loam soil in a greenhouse and were destructively harvested 9, 17, 24, 31, 38, and 45 days after emergence. Cheatgrass had greater (P<0.05) plant height, leaf area, total shoot dry weight, primary root length, number and order of branching of the second group of seminal roots, order of branching of the first group of adventitious roots, and total root dry weight than Hycrest, Whitmar, and Secar. Hycrest had greater (P<0.05) seedling growth than Whitmar and Secar. The pattern of root and shoot development was similar in the 4 species; however, species differed in the cumulative growing degree days required to initiate elongation and branching of seminal and adventitious roots. The close association between the pattern of root development and shoot growth in the 4 species may be useful in deriving models of root morphological development based on shoot development.

Key Words: Agropyron desertorum × A. cristatum, Hycrest, crested wheatgrass, Pseudoroegneria spicata, Whitmar, bluebunch wheatgrass, Elymus lanceolatus, Secar, Snake River wheatgrass, Bromus tectorum, cheatgrass, seedling establishment, root morphology

Rapid development of extensive root systems is important for successful plant establishment and growth in rangeland environments (Plummer 1943, Harris 1967, Briske and Wilson 1977, Coyne and Bradford 1985, Newman and Moser 1988). Rapid initial development of roots enables seedlings to acquire the necessary water and nutrients for growth (Brock 1986). Rapid elongation and deep penetration of seminal roots into the soil profile and the development of adventitious roots facilitate successful establishment of range grasses (Esau 1960, Hyder et al. 1971, Briske and Wilson 1977). However, few studies have attempted to quantitatively characterize seedling root morphology of range grasses and relate these characteristics to shoot development.

Detailed studies of the seedling root system of range grasses are needed to determine the developmental history of the root system in relation to shoot development. Specific studies of seedling root development and their relation to shoot development have been conducted for wheat (Klepper et al. 1984, Rickman et al. 1985). In these studies, individual axes of seminal and adventitious roots were identified and related to shoot development. The technique of Klepper et al. (1984) may be beneficial to quantitatively characterize root morphological development in range grasses with seedling morphological development similar to wheat. Identification of important root morphological characteristics may be useful in the breeding and improvement of species for rangeland seeding. In addition, documenting the relationship between shoot and root development represents a first step in accurately predicting timing of root axis development based on shoot development progression.

The objective of the present study was to compare seedling shoot and root developmental characteristics of an aggressive annual invader (cheatgrass) with a vigorous, improved hybrid grass ('Hycrest') and 2 native grass cultivars ('Whitmar' and 'Secar').

Materials and Methods

This experiment was conducted in a greenhouse at Logan, Utah, during June and July in 1987. No artificial lighting was provided, and air temperatures were maintained between 28 and 38° C. Seeds of 'Hycrest', a cultivar of hybrid crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult. × A. cristatum (L.) Gaert.]; 'Whitmar', a cultivar of bluebunch wheatgrass [Pseudoroegneria spicata (Pursh) Love subspecies inermis (Scrib. and Smith) Löve]; 'Secar', a cultivar of Snake River wheatgrass [Elymus lanceolatus (Scribner & J.G. Smith) Gould]; and cheatgrass [Bromus tectorum L.] (obtained from a site near Pullman, Wash.) were germinated on
moistened blotter paper at 25°C with a 12-h photoperiod. Seeds were considered to have germinated when the radicle was 2 mm long.

Plastic pots (20-cm diameter and 20-cm height) were filled with 8 kg of a Kidman fine sandy loam (coarse-loamy mixed mesic Calcic Haploxeroll) series previously steamed for 4 hours. The soil was watered to field capacity, and 5 germinated seeds were transplanted approximately 1-cm deep in each pot. After the seedlings produced their first foliar leaf, pots were thinned to 3 seedlings. When seedlings developed 2 main stem leaves, each pot was thinned to 1 seedling. Seedlings were allowed to grow for 45 days after emergence. Each pot was weighed every 2 days to maintain soil water at field capacity. For reference, soil water by weight for this soil was 6.7 kg kg⁻¹ at −0.03 MPa and 3.6 kg kg⁻¹ at −1.5 MPa. Deionized water was used during the first 15 days after transplanting, and 0.25 strength Hoagland solution was used thereafter.

The following equation was used to calculate growing degree days (GDD) during each 24-hour interval (Wilkins et al. 1984):

\[
GDD = \frac{(T_{\text{max}} + T_{\text{min}} - T_b)}{2}
\]

where \(T_{\text{max}}\) is the maximum air temperature in °C, \(T_{\text{min}}\) is the minimum air temperature in °C, and \(T_b\) is the base temperature below which no appreciable growth occurs. For this study \(T_b\) was assumed to be 0°C. Cumulative growing degree days (CGDD) were calculated as the total GDD accumulated after seedling emergence.

Leaf and tiller development was evaluated every other day using the system of Klepper et al. (1982) in which leaves are numbered acropetally L₁, L₂, L₃, etc. (Fig. 1). Tillers on the main stem are identified by the number assigned to the leaf that subtends them. For example, T₁ (tiller 1) is produced from the bud in the axil of L₁, T₂ (tiller 2) is produced from the bud in the axil of L₂, etc. In this system, the coleoptile is designated as L₀, and the coleoptile tiller as T₀. In fact, the coleoptilar node may be the second (Esau 1965) or third (Avery 1930, McCall 1934) node on the axis. The first leaf of tiller 1 is identified with 2 digits (L₁1), the second leaf of tiller 1 is L₁2, etc. Tillers on the main stem are designated with 1 digit, subtillers with 2 digits, and sub-subtillers with 3 digits.

Root development was quantified using the method of Klepper et al. (1984), which is based on the relation of roots to specific nodes. Each node is divided into 4 quadrants (A, B, X, and Y) with respect to the midrib of the leaf (Fig. 2). Quadrant A is to the left of the midrib, quadrant B is to the right of the midrib, quadrant X is located towards the midrib, and quadrant Y is away from the midrib. Using this method (Fig. 1), the primary root (R) which develops from the radicle, is the only root not associated with a specific node. No roots were initiated from the coleoptilar node (node 0). Roots from the epiblast "node" (the epiblast is considered by some not to be a true node) are designated with a -1, and roots from the scutellar node are designated with a -2. Roots associated with foliar nodes have positive numbers. All roots longer than 2 mm were counted. The order (degree) of branching was evaluated using 0, 1, 2, and 3 for unbranched, first-order (primary), second-order (secondary), and third-order (tertiary) branching, respectively. Although the root classification system of Klepper et al. (1984) uses a naming system that identifies roots by their relationship to specific nodes rather than designating roots as seminal and crown, nodal, or adventitious roots, in this paper we also indicate roots by these more traditional names for relating to earlier literature. However, it should be recognized that these traditional names are subject to various definitions and misinterpretation, as discussed by Klepper et al. (1984).

Seedlings were harvested at 9, 17, 24, 31, 38, and 45 days after emergence. To determine the relationship among leaves, tillers, and roots, plants were washed and then dissected under a low magnification (x10 to x50) microscope at each sampling date. The experiment was arranged in a split plot design with dates as main plots and species as subplots with 10 replications per treatment. Analysis of variance (Steel and Torrie 1980) and Least Significant Difference (LSD) multiple comparison tests were used to determine significance among treatment means. The 17 root pattern parameters determined in this study included: length and order of branching of the primary root; number, length, and order of branching of the first group of seminal roots (those associated with the scutellar node, -2); number, length, and order of branching of the first group of adventitious roots (those associated with the first foliar node, -1); number, length, and order of branching of the second group of adventitious roots (those associated with the epiblast node, -1); number, length, and order of branching of the first group of adventitious roots (those associated with node 1, the first foliar node); number, length, and order of branching of the second group of adventitious roots (those associated with the second foliar node); number, length, and order of branching of the third group of adventitious roots (those associated with node 3, the third foliar node). A discriminant analysis procedure (Afifi and Clark 1984) was used to select the root pattern characteristics that were most important for distinguishing among the

![Fig. 1. Diagram of a grass seedling showing the acropetal identification of leaves (L) and tillers (T) associated with the various foliar nodes (1 to 5).](image-url)
Adventitious roots. Only results from these 4 root characteristics will be reported.

Dry weight (oven-dried at 60°C for 48 h), total root length (Comair primary root length, number and order of branching of the second group of seminal roots (node -1), and adventitious roots (node 1) for seedlings of cheatgrass, Hycrest, and Whitmar at 45 days.

Table 1. Mean and standard deviation of the diameter (mm) of the main axis and first-order branched roots for the primary root, second group of seminal roots (node -1), and adventitious roots (node 1) for seedlings of cheatgrass, Hycrest, and Whitmar at 45 days.

<table>
<thead>
<tr>
<th></th>
<th>Diameter</th>
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<tbody>
<tr>
<td></td>
<td>Cheatgrass</td>
<td>Hycrest</td>
<td>Whitmar</td>
</tr>
<tr>
<td><strong>Primary Root</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main axis</td>
<td>0.16 ± 0.07</td>
<td>0.21 ± 0.08</td>
<td>0.20 ± 0.06</td>
</tr>
<tr>
<td>First-order branched</td>
<td>0.11 ± 0.04</td>
<td>0.14 ± 0.04</td>
<td>0.14 ± 0.02</td>
</tr>
<tr>
<td><strong>Second group of seminal roots</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main axis</td>
<td>0.18 ± 0.03</td>
<td>0.24 ± 0.07</td>
<td>0.18 ± 0.05</td>
</tr>
<tr>
<td>First-order branched</td>
<td>0.11 ± 0.02</td>
<td>0.018 ± 0.03</td>
<td>0.13 ± 0.02</td>
</tr>
<tr>
<td><strong>Adventitious roots</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main axis</td>
<td>0.52 ± 0.08</td>
<td>0.77 ± 0.01</td>
<td>0.68 ± 0.16</td>
</tr>
<tr>
<td>First-order branched</td>
<td>0.16 ± 0.04</td>
<td>0.26 ± 0.03</td>
<td>0.22 ± 0.07</td>
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Development and elongation of the primary root and the seminal roots occurred at the same time as the first leaves on the main stem, but adventitious roots appeared much later after the leaves on the first tiller had fully developed. Whitmar and Secar exhibited nearly the same seedling development. Consequently, data for these 2 cultivars were combined (Fig. 5). The roots commonly observed for these species were the primary root (R); the first group of seminal roots (those associated with the scutellar node) -2A and -2B; and the second group of seminal roots (those associated with the epiblast node) -1A, -1B, -1Y, and -1X. The primary root elongated at germination and was followed by -2A and -2B seminal root axes. Root axes -2A and -2B elongated almost simultaneously with no indication that 1 root axis preceded another. The first significant differences in total root length and root dry weight were observed among the 3 perennials during the first 910 CGDD. However, at 1090 CGDD, total root length of Hycrest was significantly greater than that of Secar and Whitmar. Number and order of branching of seminal roots associated with the epiblast node was greatest for cheatgrass throughout the entire experiment, and at 1090 CGDD, Hycrest was superior to Whitmar and Secar for both of these characteristics. Cheatgrass also had the greatest primary root length after 565 CGDD and the greatest order of branching of adventitious roots after 394 CGDD. Primary root lengths did not differ among Hycrest, Whitmar, and Secar. Order of branching of adventitious roots associated with the first foliar node of cheatgrass was greater than that of Whitmar and Secar beginning at 745 CGDD. This difference was maintained to the end of the experiment. Cheatgrass and Hycrest did not differ in order of branching of adventitious roots and neither did Whitmar and Secar.

Secar and Whitmar had a significantly greater proportion of root dry weight to total dry weight than Hycrest and cheatgrass, indicating a proportionally greater allocation of carbon resources to the roots compared to the shoots for Secar and Whitmar (Fig. 4). Significant differences were not detected among the 4 species for mean root and shoot relative growth rates. Root diameters for the primary root, second group of seminal roots, and adventitious roots were generally smaller for cheatgrass compared to those for Hycrest or Whitmar (Table 1). This apparent difference in root diameter was greatest for the main axis of the adventitious roots, suggesting that cheatgrass may allocate less carbon and nutrients per given root length than Hycrest or Whitmar.

Results

Seedling Root and Shoot Characteristics

The 4 species did not differ in the characteristics examined at the lower number of cumulative growing degree days (CGDD) but did differ significantly (P<0.05) as CGDD increased (Fig. 3). No differences were detected among species for plant height and leaf area during the first 394 CGDD after emergence. However, from 565 CGDD after emergence until the end of the experiment, Hycrest was taller than Whitmar, Secar, and cheatgrass. Leaf area of cheatgrass was greater than that of Whitmar and Secar beginning at 745 CGDD, Leaf area of Hycrest exceeded that of Whitmar and Secar at 910 and 1090 CGDD.

Total root length and root dry weight of cheatgrass were greater than those of the other 3 species starting at 745 CGDD, and these differences increased at the remaining 2 sampling dates (Fig. 3). No significant differences in total root length and root dry weight were observed among the 3 perennials during the first 910 CGDD. However, at 1090 CGDD, total root length of Hycrest was significantly greater than that of Secar and Whitmar. Number and order of branching of seminal roots associated with the epiblast node was greatest for cheatgrass throughout the entire experiment, and at 1090 CGDD, Hycrest was superior to Whitmar and Secar for both of these characteristics. Cheatgrass also had the greatest primary root length after 565 CGDD and the greatest order of branching of adventitious roots after 394 CGDD. Primary root lengths did not differ among Hycrest, Whitmar, and Secar. Order of branching of adventitious roots associated with the first foliar node of cheatgrass was greater than that of Whitmar and Secar beginning at 745 CGDD. This difference was maintained to the end of the experiment. Cheatgrass and Hycrest did not differ in order of branching of adventitious roots and neither did Whitmar and Secar.

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Root and Shoot Developmental Relationships

Whitmar and Secar

Development and elongation of the primary root and the seminal roots occurred at the same time as the first leaves on the main stem, but adventitious roots appeared much later after the leaves on the first tiller had fully developed. Whitmar and Secar exhibited nearly the same seedling development. Consequently, data for these 2 cultivars were combined (Fig. 5). The roots commonly observed for these species were the primary root (R); the first group of seminal roots (those associated with the scutellar node) -2A and -2B; and the second group of seminal roots (those associated with the epiblast node) -1A, -1B, -1Y, and -1X. The primary root elongated at germination and was followed by -2A and -2B seminal root axes. Root axes -2A and -2B elongated almost simultaneously with no indication that 1 root axis preceded another. The first

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1 Mention of a trademark, proprietary product, or vendor does not constitute guarantee or warranty of the product by the U.S. Department of Agriculture and Utah State University and does not imply approval to the exclusion of other products or vendors that may also be suitable.
Fig. 3. Shoot and root characteristics for seedlings of cheatgrass, Hycrest, Whitmar, and Secar in relation to cumulative growing degree days and days after emergence. Each point represents the mean of 10 seedlings.

group of seminal roots started elongating when the first leaf on the main stem (L1) was fully developed. The second group of seminal roots initiated elongation about when the second leaf on the main stem (L2) was fully developed. The seminal root axis Y elongated first, followed by -1A, -1B, and -1X. Adventitious roots associated with the first foliar node (first group of adventitious roots) elongated after the first leaf of tiller 1 (L1) was fully developed. Roots associated with the first foliar node initiated growth of first order branches when L12 was almost fully developed.

**Hycrest**

Hycrest followed a similar developmental pattern, with slight differences in the appearance of seminal roots. For Hycrest, semi-
nal roots -2A and -2B followed the primary root, and these were followed subsequently by roots -1A, -1B, -1X, and -1Y. The first group of seminal roots (roots associated with the scutellar node) elongated after L1 was fully developed (Fig. 5). Root axes -1A and -1B from the second group of seminal roots elongated after L2 was fully developed, followed by -1Y and -1X seminal roots. Roots associated with the first foliar node elongated after tiller 1 (T1) had fully developed its first leaf (L11).

**Cheatgrass**

Cheatgrass root development was earlier than the other species, and the sequence of root and shoot development also differed. The roots of cheatgrass commonly observed included the primary root and seminal roots -2A and -2B, while -2Y roots were not as common. Root axes -2A and -2B from the first group of seminal roots elongated after L1 was fully developed (Fig. 5). At the same time, root axes -1A and -1B from the second group of seminal roots also started to elongate, and -1Y and -1X buds were visible. Adventitious roots associated with the first foliar node, 1A, 1B, 1X, and 1Y, started to elongate by the time L11 began elongation at T1. The root axes oriented to the left and right of the leaf midrib tended to elongate first. Adventitious roots initiated first order branching after L12 was fully developed.

**Species Comparisons**

Although root and shoot developmental relationships were generally similar for the 4 species, they differed significantly in their CGDD requirements for initiating seminal and adventitious roots as well as in their timing of root branching (Fig. 5). For example, Whitmar and Secar required approximately 910 CGDD for well-developed second order branching of seminal roots, whereas Hycrest and cheatgrass required only 745 and 565 CGDD, respectively, to reach the same developmental stage.

**Discussion**

The technique of Klepper et al. (1984) worked well for quantitatively characterizing root morphological development in Hycrest, Whitmar, Secar, and cheatgrass. Although this technique was time consuming, it provided a quantitative assessment of the morphological development of roots in these grasses. Although number and order of branching of the second group of seminal roots and order of branching of the first group of adventitious roots would be quite time consuming to evaluate in a plant breeding and selection program, primary root length might be 1 root characteristic that would be relatively fast and straightforward to assess. Consequently, primary root length would certainly be worth exploring as a possible selection criterion in a range grass breeding program.
The 4 range grasses evaluated in our study all exhibited a phasic pattern of root elongation and branching in relation to shoot development. These root and shoot relationships were similar to those reported for wheat (Klepper et al. 1984, Rickman et al. 1985). In winter wheat, seminal and adventitious root axes elongated and initiated branching in a predictable order and were closely associated with patterns of leaf development. These relationships have allowed the development of models of root axis development in cereals (Rickman et al. 1985). The phasic pattern of root axis elongation and branching in relation to shoot development observed for the 4 range grasses in our study also could be used to derive models of root axis appearance and branching pattern development. The most important parameters to include in such a model for these range grasses would be: sequential leaf development on the main stem, tiller development, and timing of elongation and branching of seminal and adventitious root axes. Harris (1967) examined root depth, number of roots, and leaf growth of cheatgrass and bluebunch wheatgrass in the field. Although Harris (1967) did not examine root morphological development in relation to shoot development, he found that cheatgrass had greater root growth than bluebunch wheatgrass and that this greater root growth generally was associated with greater leaf growth. In the present study, cheatgrass consistently exhibited greater total root length than Hycrest, Whitmar, and Secar, and this greater root length also was associated with more rapid leaf and tiller development and greater leaf area. Rapid shoot development in cheatgrass was associated with earlier branching of the primary root, a greater number and order of branching of seminal roots, and earlier elongation and branching of adventitious roots.

Elongation of seminal and adventitious root axes are important in seedling performance, although seedling establishment depends ultimately on the elongation of adventitious roots (Esau 1960). Newman and Moser (1988) observed that adventitious roots of big bluestem (Andropogon gerardii Vitman var. gerardii), Indiangrass [Sorghastrum nutans (L.) Nash], and switchgrass (Panicum virgatum L.) initiated elongation 4 weeks after planting. Wilson and Briske (1979) observed that initiation of adventitious roots in blue grama [Bouteloua gracilis (Wild. ex Kunth) Lagasca ex Griffiths] enhanced seedling establishment. In the present study, cheatgrass elongated and initiated branching of adventitious roots about 1 week earlier than Hycrest, Whitmar, and Secar. Early elongation and branching of adventitious root axes in cheatgrass probably contributed to enhanced aboveground growth and seedling performance through increased absorption of water and soil nutrients.

The smaller root axis diameter in cheatgrass compared to Hycrest and Whitmar could be an advantage for cheatgrass in production of greater root length than Hycrest or Whitmar with the same quantity of carbon resources. This is supported by the work of Svejcar (1990), who found that cheatgrass was more efficient (per unit of biomass) in producing leaf area and root length than Agropyron desertorum. In our study, cheatgrass also had a smaller proportion of root to total dry weight than Whitmar and Secar. Greater resource allocation to the shoot than the root cheatgrass may have allowed an earlier development of photosynthetic tissue and subsequently greater seedling growth for cheatgrass compared to Whitmar and Secar. The greater seedling growth of Hycrest compared to Whitmar and Secar was related to its faster leaf area production and earlier and faster seminal and adventitious root elongation and branching than Secar and Whitmar. In conclusion, this present study in conjunction with results of Aguirre and Johnson (1991) and Johnson and Aguirre (1991) indicate that root morphological development is important in enabling range grass seedlings to establish.

Literature Cited


