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Seedling Root Development and Morphology of Cool-Season and Warm-Season Forage Grasses

P. R. Newman and L. E. Moser*

ABSTRACT

A detailed description of grass seedling root morphology is essential to understand the differences in the establishment process among grasses. A repeated greenhouse study using a 1:1 mixture of Sharpsburg silty clay loam (fine, montmorillonitic, mesic Typic Argiudolls) and coarse sand was conducted to determine root morphology differences at the third-leaf stage among nine cool-season forage grasses, creeping foxtail (*Alopecurus arundinaceus* Poir.), reed canarygrass, (*Phalaris arundinacea* L.), smooth brome grass (*Bromus inermis* Leyss.), tall fescue (*Festuca arundinacea* Schreb.), orchardgrass (*Dactylis glomerata* L.), russian wildrye (*Elymus junceus* Fish.), crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], intermediate wheatgrass [*A. intermedium* (Host) Beauv.], and western wheatgrass (*A. smithii* Rydb.); and nine warm-season forage grasses, sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], blue grama [*B. gracilis* (H.B.K.) Lag. ex. Steud.], sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], big bluestem (*Andropogon gerardii* var. *gerardii* Vitman), sand bluestem [*A. gerardii* var. *paucipilus* (Nash) Fern.], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], caucasian bluestem [*Bothriochloa caucasica* (Trin.) C.E. Hubb.], indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). These grasses were selected as representative forage grasses of the northern USA. Andropogoneae species reached third leaf emergence 3 to 5 days earlier than other warm-season grasses and 3 to 15 days earlier than cool-season grasses. Most cool-season grasses had no or little subcoleoptile internode elongation except Aveneae species. Aveneae species and warm-season grasses, except Chlorideae species, had root development from the subcoleoptile internode. Sand bluestem had less subcoleoptile internode root development than big bluestem. Seminal root development was greater in species of the Triticeae tribe. Adventitious root development occurred by the three-leaf stage on species of all tribes except for Andropogoneae members. Most grasses were in a juvenile period of root growth at third leaf emergence. Stage of root development did not coincide with stage of shoot development among species.

Additional index words: Gramineae, Seedling root morphology, Subcoleoptile internode roots, Transitional node roots, Permanent roots, Adventitious roots, Seminal roots.

INFORMATION is lacking on seedling root morphology of forage grasses (Hyder et al., 1971). A detailed description of seedling root morphology of a diverse group of forage grasses provides a base for understanding the establishment process in grasses.

Hoshikawa (1969) studied the underground organs of Gramineae seedlings to establish relationships between seedling root morphology and the systematics of grasses. He classified 219 species into six seedling types based on root morphology and noticed that nearly all species of the same genus were of the same seedling type. Most of the warm-season grasses ("Panicoid" seedling type) had an elongated subcoleoptile internode with subcoleoptile internode root development. The cool-season grasses ("Festucoid" seedling type) lacked or had little subcoleoptile internode elongation and had transitional-node (seminal) root development.

The subcoleoptile internode (SCI) (Fig. 1) was described as the first internode of the grass seedling shoot (Boyd and Avery, 1936) or the internode below the coleoptile node and above the scutellar node (Hyder et al., 1971). Hyder et al. (1971) described SCI roots

as adventitious roots that develop from the SCI. Subcoleptile internode elongation positions the seedling crown in relation to the soil surface. Hoshikawa (1969) described transitional node roots as roots that develop from the scutellar node (seed node) and the primary root as the resulting root when the radicle of the grass seed embryo developed. The primary root was usually the first root to emerge from the germinating grass seed, followed by transitional node roots (Hoshikawa, 1969). Adventitious roots develop in a succession of whorls from the lower nodes of the stem (Onderdonk and Ketcheson, 1972). The lower nodes are often collectively called the *seedling crown* (Hayward, 1938). The adventitious roots become the major root system of the established grass seedling (Metcalf and Nelson, 1985).

Hyder et al. (1971) related the seedling failures of blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex Steud.] on the semiarid plains of Colorado to seedling morphology. The lack of SCI elongation in crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] placed the seedling crown, the site of origin of the adventitious roots, at the seeding depth. With SCI elongation, the blue grama seedling crown was placed near the soil surface. The more successful establishment of crested wheatgrass compared to blue grama was explained by the more favorable plant-soil water relations at the seeding depth than at the soil surface.

The objective of our study was to describe the seedling root development and morphology of a group of economically important forage grasses in an effort to understand how the establishment process may vary among species.

MATERIALS AND METHODS

Nine cool-season and nine warm-season grasses (Table 1) were studied in a greenhouse experiment that was repeated once. Cool-season grasses included 'Garrison' creeping foxtail (*Alopecurus arundinaceus* Poir.), reed canarygrass (*Phalaris arundinacea* L.), 'Lincoln' smooth brome grass (*Bromus inermis* Leyss.), 'Kentucky 31' tall fescue (*Festuca arundinacea* Schreb.), 'Potomac' orchardgrass (*Dactylis glomerata* L.), 'Vinall' russian wildrye (*Elymus junceus* Fish.), 'Ruff' crested wheatgrass, 'Slate' intermediate wheatgrass [*Agropyron intermedium* (Host) Beauv.], and 'Nebraska 1' western wheatgrass (*A. smithii* Rydb.). The warm-season grasses selected were 'Trailway' side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], 'Southern' blue grama, 'Nebraska 27' sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], 'Pawnee' big bluestem (*Andropogon gerardii* var. *gerardii* Vitman), 'Goldstrike' sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.], 'Camper' little bluestem [*Schizachyrium scoparium* (Michx.) Nash], caucasian bluestem [*Bothriochloa caucasica* (Trin.) C.E. Hubb.], and indiangrass [*Sorghastrum nutans* (L.) Nash].

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Table 1. Days to third leaf emergence and means of seven seedling root morphology parameters of nine cool-season and nine warm-season grasses.

Cool-season grasses:										
Tribe—Species	Common name	Third leaf emerg. †	SCI elong.	Seedling root morphology parameters						
				SCIR‡	Seminal roots	Juvenile roots§	Adventitious roots			
		d		% of plts.	no./plt.		mg/plt.	% of plts.	no./plt.	mg/plt.
Cool-season grasses:										
Aveneae										
<i>Alopecurus arundinaceus</i>	Creeping foxtail	23–22	Yes	20.6	0.5	0.2	0.5	95.7	4.5	0.7
<i>Phalaris arundinacea</i>	Reed canarygrass	20	Yes	82.0	3.1	0.4	1.0	100.0	5.6	1.5
Poeae										
<i>Bromus inermis</i>	Smooth brome	30–28	Yes¶	0.0	0.0	0.9	4.7	100.0	4.2	5.2
<i>Festuca arundinacea</i>	Tall fescue	30–28	Yes¶	0.4	0.0	0.7	2.3	99.4	4.3	3.1
<i>Dactylis glomerata</i>	Orchardgrass	22–24	Yes	3.9	0.1	0.1	1.5	100.0	3.8	1.3
Triticeae										
<i>Elymus junceus</i>	Russian wildrye	30–24	No	0.0	0.0	0.9	2.7	83.7	1.1	0.7
<i>Agropyron cristatum</i>	Crested wheatgrass	20	Yes¶	0.9	0.0	1.8	1.7	61.0	1.5	0.4
<i>Agropyron intermedium</i>	Intermediate wheatgrass	22–24	Yes¶	0.5	0.0	1.7	7.4	69.4	1.2	1.3
<i>Agropyron smithii</i>	Western wheatgrass	30–28	Yes¶	0.0	0.0	0.9	2.4	93.9	2.3	1.6
Warm-season grasses:										
Chlorideae										
<i>Bouteloua curtipendula</i>	Sideoats grama	20	Yes	6.7	0.1	0.3	0.8	82.2	0.9	0.4
<i>Bouteloua gracilis</i>	Blue grama	20–22	Yes	4.3	0.0	0.2	0.6	91.4	0.9	0.2
Eragrostaeae										
<i>Eragrostis trichodes</i>	Sand lovegrass	20–19	Yes	100.0	7.7	0.0	0.4	91.6	1.8	0.3
Andropogoneae										
<i>Andropogon gerardii</i> var. <i>gerardii</i>	Big bluestem	15–16	Yes	92.8	3.3	0.2	1.9	0.1	0.1	0.0
<i>Andropogon gerardii</i> var. <i>paucipilus</i>	Sand bluestem	17–15	Yes	71.3	1.4	0.4	1.5	3.8	0.1	0.0
<i>Schizachyrium scoparium</i>	Little bluestem	17–15	Yes	87.0	3.3	0.1	0.9	1.6	0.0	0.0
<i>Bothriochloa caucasica</i>	Caucasian bluestem	15	Yes	98.9	9.3	0.5	1.0	1.1	0.1	0.0
<i>Sorghastrum nutans</i>	Indiangrass	17–15	Yes	90.0	3.2	0.4	1.9	0.0	0.0	0.0
Paniceae										
<i>Panicum virgatum</i>	Switchgrass	22–24	Yes	97.7	3.9	0.7	2.7	79.7	1.0	0.4
LSD (0.05)				19.2	0.8	0.5	0.5	17.7	0.9	0.8

† Range of days to 50% third leaf emergence. The first and second number represents Exp. 1 and 2, respectively. A single number means that the time of third leaf emergence was the same for both experiments.

‡ SCIR = subcoleoptile internode roots.

§ Juvenile root weight includes primary root, seminal roots, subcoleoptile internode, and SCIR.

¶ Less than 5-mm subcoleoptile internode elongation.

riochloa caucasica (Trin.) C. E. Hubb.], 'Holt' indiangrass [*Sorghastrum nutans* (L.) Nash], and 'Pathfinder' switchgrass [*Panicum virgatum* L.]. There were species from three cool-season and four warm-season grass tribes represented (Gould and Shaw, 1983).

Plastic pots 17 cm in diameter by 15 cm deep were filled with a 1:1 mix of Sharpsburg silty clay loam and coarse sand. Pots were arranged in a completely randomized experimental design with four replications. Each experimental unit was a pot with 25 pure live seeds planted 2.0 cm deep. The 2.0 cm depth was used to cause seedling subcoleoptile internode elongation. The pots were subirrigated for 1 h daily. Temperatures ranged from 28°C d to 23°C night. The temperature conditions allowed rapid healthy growth of both the warm- and cool-season grasses. Photoperiod was extended to a 14-h d with two 400-W metal halide lamps to produce an irradiance of 55 W m⁻².

When half of the emerged seedlings of a species in each replicate reached third leaf emergence, data were taken in all four replicates of that species. All of the seedlings from each pot were carefully washed and nearly all roots were retained. They were placed in a 28 by 32 cm plastic bag to maintain moisture. The plastic bags containing the seedlings were stored at 5°C until measurements were taken within 3 d of sampling. Before morphological parameters were recorded, the seedlings were washed briefly in soapy water to remove adhering soil. Procedures were identical when the experiment was repeated. A sketch showing root development of each species was made from a representative seed-

ling (Newman, 1986). Percentage of seedlings per pot with subcoleoptile internode roots, subcoleoptile internode root number, seminal root number, juvenile root dry weight (the combination of primary root, subcoleoptile internode and its roots, and seminal roots), percentage of seedlings per pot with adventitious roots, number of adventitious roots, and adventitious root dry weight were determined. Days to third leaf emergence from the second collar for 50% of the population for each grass were recorded. Third leaf emergence was the day when the third leaf was first visible. Three seedlings that were at the third-leaf stage for each experimental unit were used for measurement and data were averaged for analysis. Seedlings were dried at 45°C for 48 h to determine root dry weights.

Data from both experiments were combined because only three of the seven parameters showed a significant ($P > 0.01$) experiment \times species interaction and these interactions were very small. Treatment means were subjected to the least significant difference (LSD) test. The appropriate error mean square to test the species nested in tribe within subfamily effect was used in calculating the LSD.

In order to simplify discussion, we are using the term *seminal roots* to describe those roots that originate at the scutellar node or near the seed and that are not part of the primary root or arise from the SCI. Hoshikawa (1969) referred to them as transitional node roots. We are using subcoleoptile internode (SCI) for the internode between the scutellar and coleoptilar nodes that has been called a *mesocotyl* by Hoshikawa (1969). The SCI is a unique structure

unlike either the root or the stem. The general term *adventitious roots* is used to refer to roots coming from the coleoptilar node that form the major root system of a grass plant. These adventitious roots have been called several names including *permanent roots* (Hayward, 1938), *cotyledonary node roots* (Hoshikawa, 1969), and *crown roots* (Taylor and McCall, 1936).

RESULTS AND DISCUSSION

Warm-season grasses reached third leaf emergence in 15 to 24 d, whereas cool-season grasses reached third leaf emergence 20 to 30 d from planting (Table 1). Members of the Andropogoneae tribe reached third leaf emergence 3 to 8 d earlier than other warm-season grass species. None of the cool-season grasses could be grouped by tribe with time to third leaf emergence (Table 1). Reed canarygrass reached third leaf emergence 2 to 3 d earlier than creeping foxtail. Orchardgrass reached third leaf emergence 4 to 8 d earlier than smooth brome and tall fescue. Western wheatgrass was 4 to 8 d later than crested and intermediate wheatgrasses in reaching third leaf emergence. Crested wheatgrass was the earliest of the Triticeae tribe to reach third leaf emergence. The only major difference in third leaf emergence between experiments was with russian wildrye, which reached third leaf emergence 6 d earlier in Exp. 2 than in Exp. 1.

Subcoleoptile internode roots (SCIR) were present on 71 to 100% of the seedlings of the Eragrostae, Andropogoneae, and Paniceae tribes. Cool-season grasses had little subcoleoptile internode root development. Both members of the Aveneae tribe, creeping foxtail and reed canarygrass, had a greater SCI root development than other cool-season grasses. Both species of the Chlorideae tribe had limited SCI root development. A lower percentage of sand bluestem had SCIR than big bluestem.

Subcoleoptile internode root number was greatest on caucasian bluestem and sand lovegrass than on other grasses. Reed canarygrass had more SCIR than other cool-season grasses since it had a long SCI. Although creeping foxtail had a long SCI, it had less SCIR than reed canarygrass, and the SCIR were concentrated at the acropetal end of the SCI. The SCIR were spaced evenly on the SCI of reed canarygrass. Other cool-season grasses and species of the Chlorideae tribe had no or very limited SCIR development. Smooth brome had intracoleoptile internode elongation (second or third internode elongation), but it was not so obvious as with intermediate wheatgrass. This resulted in some confusion in identifying roots that developed from below the seedling crown. For smooth brome they were considered adventitious roots.

Seminal root number was greatest on members of the Triticeae tribe. Crested wheatgrass and intermediate wheatgrass had one to two seminal roots, and russian wildrye and western wheatgrass averaged one seminal root. The determination of seminal roots is difficult and they may be confused with SCIR growing at the basipetal end of the SCI or branch roots of the primary root near the seed (Fig. 1).

The juvenile root mass of intermediate wheatgrass was the greatest among all species studied. The difference between crested wheatgrass and intermediate wheatgrass in juvenile root weight appeared to be due

to the relative size and branching of the seminal and primary roots, since both had a similar number of seminal roots. The high-juvenile root mass value for smooth brome may actually be due to its extensive primary root development, or it may have resulted from misidentified seminal roots that were actually adventitious roots that had developed from node(s) near the seed.

Adventitious roots were present on 70 to 100% of the seedlings of all tribes except those of crested wheatgrass and intermediate wheatgrass and members of the Andropogoneae tribe. Members of the Andropogoneae developed to the third leaf emergence stage quickly and were harvested 3 to 5 d earlier than the other warm-season grasses. Members of the Andropogoneae had 85 to 98% less adventitious root development than other warm-season grass species studied. Andropogoneae species reached the third-leaf stage before adventitious development could take place.

Time from planting was associated with adventitious root development of grass seedlings. A higher percentage of seedlings of Triticeae had adventitious roots when harvested at a later date (data not shown). At 30 d from planting, 93% of the russian wildrye seedlings had adventitious root development in Exp. 1, while at 24 d from planting, only 75% of the russian wildrye seedlings had an adventitious root development in Exp. 2. Similar positive associations were found between time from planting and percentage of seedlings with adventitious roots among other species in both experiments.

Adventitious root number was greater on species of Aveneae and Poeae than on species in other tribes. Western wheatgrass had a greater adventitious root

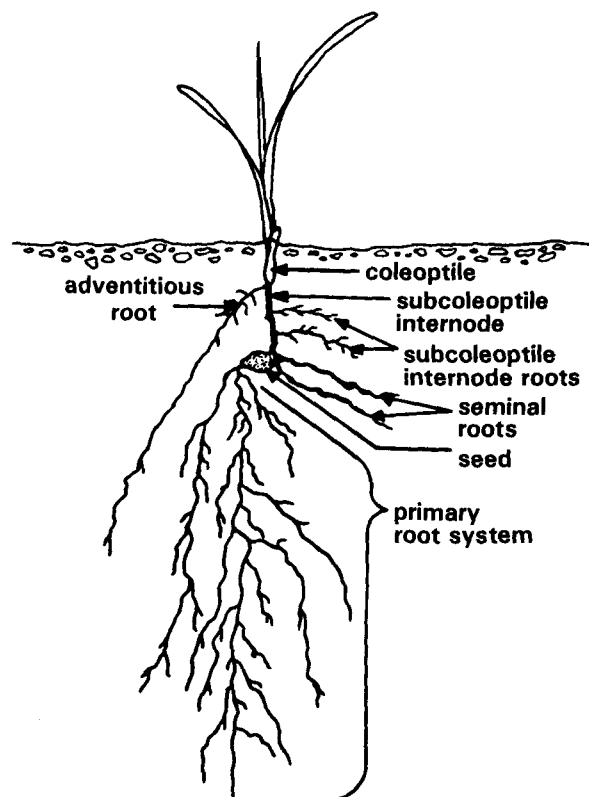


Fig. 1. Grass seedling root morphology.

number than other species of Triticeae although it was harvested 4 to 8 d later. Species of the Chlorideae, Eragrostae, and Paniceae had approximately one adventitious root at third leaf emergence. Russian wildrye and western wheatgrass were harvested 30 d from planting in Exp. 1 and 24 to 28 d from planting in Exp. 2, respectively, but Russian wildrye had one less adventitious root in both experiments. Reed canarygrass was harvested 20 d from planting in both experiments, but had the highest adventitious root number of all species studied. Apparently the leaf developmental stage of seedling shoots is not associated with adventitious root development as much as seedling age or genetic differences among species.

Adventitious root dry weight was much greater for the cool-season grasses than for warm-season grasses. The greenhouse temperature regime (28°C d and 23°C night) may have been more conducive to root growth in cool-season grasses than in warm-season grasses. Smooth brome grass and tall fescue had the highest adventitious root weight of all species studied. The adventitious root weight generally did not exceed the juvenile root weight in most of the species. Most of the species studied were still in a juvenile period of root growth at third leaf emergence. Creeping foxtail, reed canarygrass, smooth brome grass and tall fescue surpassed the 1:1 ratio of adventitious to juvenile root weight. Evidently, these grasses had progressed further in the transition from juvenile to adventitious root dependence than the other grasses at third leaf emergence.

Seedling root morphology of the cool-season grasses showed distinct differences as compared to the warm-season forage grasses at third leaf emergence. Most of the cool-season grasses had less SCI elongation, thus causing the seedling crown to form deeper in the soil. With a 2-cm planting depth, extensive subcoleoptile internode elongation occurred on all of the warm-season grasses and with species of Aveneae. Only Russian wildrye had no SCI elongation at all. There was a small amount of SCI elongation on western and crested wheatgrasses, and a small amount of intracoleoptile internode elongation in smooth brome grass and intermediate wheatgrass. All of the species studied that had SCI elongation also had SCIR development, except few SCIR were present in species of the Chlorideae tribe. Subcoleoptile internode root development may contribute to seedling establishment of species of Aveneae, Eragrostis, Andropogoneae, and Paniceae.

Primary root development plays an important role in early seedling establishment and there were differ-

ences in primary root morphology among species. Sideoats grama seedlings had a finely branched primary root system. Seedlings of creeping foxtail had little primary root development and may exemplify less emphasis on primary root development in that particular species. Since long SCI roots were concentrated toward the acropetal end of the SCI, they may have an important function in the juvenile root phase of creeping foxtail, but not in the other species.

Adventitious root development was virtually nonexistent at third leaf emergence on species of the Andropogoneae tribe, and was limited on all warm-season grass species studied. These grasses developed short leaves quickly and reached the third-leaf stage in 15 to 17 d.

The juvenile root system consisting of the primary root, seminal roots, and any subcoleoptile internode roots are important for the extremely young seedling. Determining the function of each component may be important if the juvenile root system limits seedling establishment. Rapid adventitious root initiation has been shown to be essential in seedling survival (Hyder et al., 1971). Evaluating the establishment of a young grass stand cannot be accomplished by looking at the developmental stage of the seedling shoot only, since adventitious root development varies with shoot morphology among species. Representative seedlings should be excavated carefully so that the number and extent of adventitious roots can be determined when evaluating the potential success of a grass seeding.

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