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Grass seedling morphology when planted at different depths

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Abstract

Depth of planting has been acknowledged in the literature as a factor which modifies grass seedling morphology. However, the type and extent of this modification has not been clearly documented. A growth chamber study was conducted to evaluate the mesocotyl, coleoptile, and leaf internode development of smooth bromegrass 'Lincoln' (*Bromus inermis* Leyss.), sideoats grama 'Pierre' [*Bouteloua curtipendula* (Michx.) Torr.], and western wheatgrass 'Rodan' [*Agropyron smithii* Rydb.; syn. = *Pascopyron smithii* Rydb. (Löve)] seedlings when planted at 6, 25, 51, 76, and 102-mm soil depths. Environmental conditions within the growth chamber were held constant for all treatments. Mesocotyl, coleptile, and/or leaf internodes did not elongate equally for all planting depths. Shallow-planting lessened elongation while deep planting maximized elongation within the genetic limits possible for each species and individual genotype. When evaluating grass seedling morphology, regardless of species or seed size, planting depth must be great enough to allow inherent genetic expression in the development and elongation of the mesocotyl, coleoptile, and leaf internodes. When planting for a grass stand, the sower should keep in mind that percent emergence for smooth bromegrass, sideoats grama, and western wheatgrass decreased significantly when planted deeper than 26, 8, and 52 mm, respectively. Adventitious root numbers at the coleoptilar node decreased significantly when planting depths exceeded 25, 51, and 51 mm for smooth bromegrass, sideoats grama, and western wheatgrass, respectively.

Key Words: mesocotyl, leaf internodes, coleoptile, nodes, roots, crown depth, western wheatgrass, sideoats grama, smooth bromegrass

Depth of planting has been acknowledged in the literature as a factor that modifies grass seedling morphology (Percival 1921, Avery 1930). The specific morphological changes and their magnitude as related to different planting depths and environmental conditions are still unclear. Percival (1921) reported that for wheat seedlings the first internode, the internode below the first lateral bud in the axis of the coleoptile, always remained very short. Esau (1977) named this first internode the mesocotyl of the grass seedling. Percival (1921) also found that the second, third and sometimes other internodes elongated below the crown of the wheat plant when wheat seed was planted 102 mm (4 inches) or more deep. Taylor and McCall (1936) reported that deeper planting increased the length of wheat coleoptiles and subcrown internodes. Longer mesocotyl and coleoptile lengths at deeper planting depths in other cereal and forage grasses have also been reported by Hyder et al. (1971), Turner et al. (1982), Addae and Pearson (1992). Hoshikawa (1969) studied the underground organs of 219 species of 88 genera of Gramineae. He related planting depth to seed size and planted larger-seeded species at deeper depths. This provided an evaluation of grass seedling morphological structures which developed at a planting depth likely to result in successful establishment, but did not enhance the potential maximum elongation of seedling internodes. Newman and Moser (1988) also reported changes in grass seedling morphology when planted at deeper depths and noted decreased emergence for various species when planting depths were increased.

Webb and Stephens (1936) found that placement of the crown for wheat was related to variety, environmental factors (especially temperature), and depth of seeding, Loeppky et al. (1989) found that as little as a 17 mm increase in planting depth resulted in significantly deeper crown placement for winter wheat. Poulos and Allan (1989) found the length of the subcrown internode for winter wheat was more related to planting depth than was crown depth. This may reflect the situation when wheat crown placement results from the elongation of more than 1 subcrown internode (Percival 1921, Peterson 1965).

The literature contains examples of studies with cereal and forage grasses that had greater emergence and establishment success from shallow planting depths (Mutz and Scifres 1975, Lafond and Fowler 1989, Sepaskhah and Ardekani 1978, Young 1992). Other studies had greater emergence and establishment success from deep planting (Kinsinger 1962, Tadmor and Cohen 1968, Carren et al. 1987, Hudspeth and Taylor 1961). These varying results add to the complexity of understanding the importance of planting depth to successful cereal and forage grass establishment.

Our study objective was to describe the morphological development of smooth bromegrass, sideoats grama, and western wheatgrass seedlings across a wide range of planting depths to maximize the elongation of seedling coleoptiles and internodes.

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Study Methods

A growth chamber study was conducted to evaluate the morphological development of smooth bromegrass, sideoats grama, and western wheatgrass seedlings planted at planned depths of 6, 25, 51, 76, and 102 mm. The study was conducted twice during the winter of 1987-88, with 3 observations of each planting depth during each run. Cones were placed in the growth chamber in a completely random design for each species and sample date. Cone containers (38 mm tip diameter, 209 mm long, and 2° taper with a volume of 164 cm^3) were painted black and packed with Lihen soil (sandy, mixed Entic Haploborolls) to the desired planting depth at a bulk density of 1.4 g cc^{-1}; seeded and packed with the same soil and the same bulk density to within 10 mm of the top of the cone. Seven smooth bromegrass and western wheatgrass seeds (caryopsis + lemma and palea) were planted in each cone. Average seed weight plus or minus 1 standard deviation was 2.6 ± 0.8 mg for smooth bromegrass and 4.3 ± 1.0 mg for western wheatgrass. Ten seed (caryopsis) of sideoats grama were seeded per cone and averaged 0.8 ± 0.2 mg per caryopsis.

High intensity sodium and multivapor lamps produced a photon flux density of about 1100 μ mol $m^{-2}s^{-1}$ at the plant level in the growth chamber. Air temperatures were 23-25°C during a 14 hour day^{-1} light period (0800 to 2200 hours) and from 17-19°C during a 10 hour day^{-1} dark period (2200-0800 hours). At this light flux and air temperature, the soil temperature at a depth of 38 and 76 mm in the cones was about 23 and 22.6°C, respectively, at 1230 hours. During the dark periods at 0630 hours, soil temperature was about 14.8 and 15.1°C, respectively, at the 38 and 76 mm depths. A relative humidity was held near 50% throughout the day. Nutrients were added using half-strength Hoagland's nutrient solution (100 ppm N) at watering once a week. In the first study, cones were watered daily to field capacity (25% soil water by volume) for 20 days. The emerged plants became purple and were growing slowly. Watering was reduced to maintain about 21% soil water by volume. Weekend water was eliminated after 2 weeks by watering each cone to field capacity each Friday. Plants became normal in growth and color. Under this watering level and allowing 72 hours for stabilization, the soil water content in the cone containers was about 5.2, 5.5, 5.5, and 4.9 mm of water in the 0-25, 26-51, 52-76, and 77-102 mm-soil-depths, respectively.

The number of seedlings emerging from each cone was counted and used to determine the percent emergence for each planting depth. Seedlings in each cone were thinned after emergence was complete, so only the first emerged seedling remained in each cone. Cones were sampled at 7, 14, 21, 35, 48, and 58 days after planting to evaluate sequential development. Seedlings from the first run were grown for 58 days before the final sample was taken. Since crown placement appeared complete before 58 days, the final sample for the second run was taken at 48 days. Six cones were sampled for all-planting depths at 14 days after planting and at the final sample. At each sampling, each seedling was marked at the soil surface and was carefully washed from the soil. The actual planting depth, the vertical length of its mesocotyl, coleoptile, leaf internodes, number and location of adventitious roots, and other characteristics were measured. Analysis of variance (GLM for unbalanced data) was used to determine significant depth treatment effects at 14 days after planting and at the final sample date (SAS Institute 1985). When overall differences among planting depths were significant, differences among the individual depths for that date were tested for significance using a protected Waller/Duncan test, k=100.

Results and Discussion

By 14 days after planting, almost all seedlings in this study had

Table 1. Grass seedling morphology 14 days after planting.

Depth of Planting	n	Mesocotyl	Coleoptile	Total[1]	Coleoptile Tip[2]	Days to Emergence	Emergence[3]
(mm)		---------- Vertical length (mm)	----------		----------		(%)
(Smooth Bromegrass)							
8.0[4]	6	0.5 b	12.0 b	12.5	+4.5	5.0 c	57 a
26.0	6	2.5 b	25.0 a	27.5	+1.5	6.3 b	57 a
51.5	6	3.5 ab	28.5 a	32.0	-19.5	8.7 a	21 b
77.0	6	7.0 a	25.5 a	32.5	-44.5	NE[5]	0 b
103.0	6	4.5 ab	30.0 a	34.5	-68.5	NE	0 b
(Sideoats Grama)							
8.0	6	7.0 b	6.5 a	13.5	+5.5	3.5 c	72 a
25.0	6	22.5 ab	6.0 a	28.5	+3.5	5.0 b	50 b
51.0	6	34.5 a	5.0 a	39.5	-11.5	7.3 a	7 c
77.5	6	35.0 a	5.5 a	40.5	-37.0	NE	0 c
102.5	6	31.5 a	4.5 a	35.5	-67.0	NE	0 c
(Western Wheatgrass)							
8.0	6	0.0 a	14.0 d	14.0	+6.0	5.8 c	64 a
25.0	6	0.0 a	28.0 c	28.0	+3.0	7.2 c	60 a
52.0	6	1.0 a	40.5 b	41.5	-10.5	9.5 b	60 a
77.0	6	0.0 a	47.0 a	47.0	-30.0	11.5 a	7 b
102.0	6	2.0 a	50.0 a	52.0	-50.0	NE	0 b

[1]Mesocotyl + coleoptile.
[2] Location of coleoptile tip above (+) or below (-) soil surface.
[3]% emergence observed for seedlings at 14 days after planting (smooth brome grass n=42, sideoats grams n=60, western wheatgrass n=42).
[4]All measurements rounded to nearest .5 mm; within columns, mean followed by same letter are not different at $P \leq 0.05$ (Protected Waller/Duncan test, k=100).
[5] NE - no plants emerged at 14 days after planting.

emerged. Only 3 additional western wheatgrass seedlings emerged after 14 days, and they were from 102 and 76 mm planting depths. Generally, it appears that by 14 days after planting, mesocotyls plus coleoptiles have elongated to their maximum length (Table 1). At planting depths of 51 mm or greater, no coleoptiles reached the soil surface.

Smooth bromegrass seedlings emerged from a maximum depth of 51.5 mm and these seedlings emerged by the true leaves growing through 19.5 mm of soil. Smooth bromegrass percent emergence decreased significantly when planted at 51.5 mm compared with 8 and 26-mm depths (Table 1). These emergence results are similar to those reported by Lueck et al. (1949) for 'Lincoln' smooth bromegrass seeded in the field at 25 and 51 mm (1 and 2 inches). Days to emergence increased with planting depth for all species.

Sideoats grama seedlings also emerged from planting depth of 51 mm and the true leaves of these seedlings grew through 11.5 mm of soil. However, percent emergence of sideoats grama decreased significantly with each increase in planting depth (Table 1). The observed germination and emergence in our study is similar to that reported by Olmsted (1941) when he seeded sideoats grama at a planting depth of 6 to 12 mm (0.25 to 0.5 inches) in a greenhouse study.

Western wheatgrass percent emergence was similar as planting depth increased from 8 to 52 mm. At a 52 mm-planting depth, true leaves of western wheatgrass seedlings were able to penetrate 10.5 mm of soil without a significant decrease in emergence percentage (Table 1). Western wheatgrass seedlings emerged from a planting depth of 77 mm, and at this depth the true leaves of this species had to penetrate 30 mm of soil. At this planting depth, percent emergence of western wheatgrass decreased significantly when compared with 8, 25, and 52 mm depths (Table 1).

Hyder et al. (1971) proposed that the mesocotyl and coleoptile represent the maximum depth of planting for a grass seedling, and beyond this depth, emergence will decrease significantly because true leaves are not as adapted to growing through soil as is the coleoptile. Our data indicate that differences exist between species in the ability of true leaves to penetrate soil. True leaves of western wheatgrass in our study penetrated 10.5 mm of soil without a significant decrease in emergence. In contrast, emergence of both smooth bromegrass and sideoats grama seedlings decreased when true leaves had to penetrate soil. In all cases, deeper planting resulted in more days until emergence. The length of the mesocotyl and coleoptile and position of the coleoptile tip for seedlings that did not emerge from the deeper planting depths provides an estimate of mesocotyl and coleoptile length needed to achieve emergence (Table 1).

The location of the crown of establishing grass seedlings over time is not well documented in the literature. Hyder (1974) defined the crown of a grass plant as the location where 2 or more nodes remain close together. Generally, grass seedlings are not considered established until functional adventitious roots develop enough to insure an adequate water and nutrient supply to the

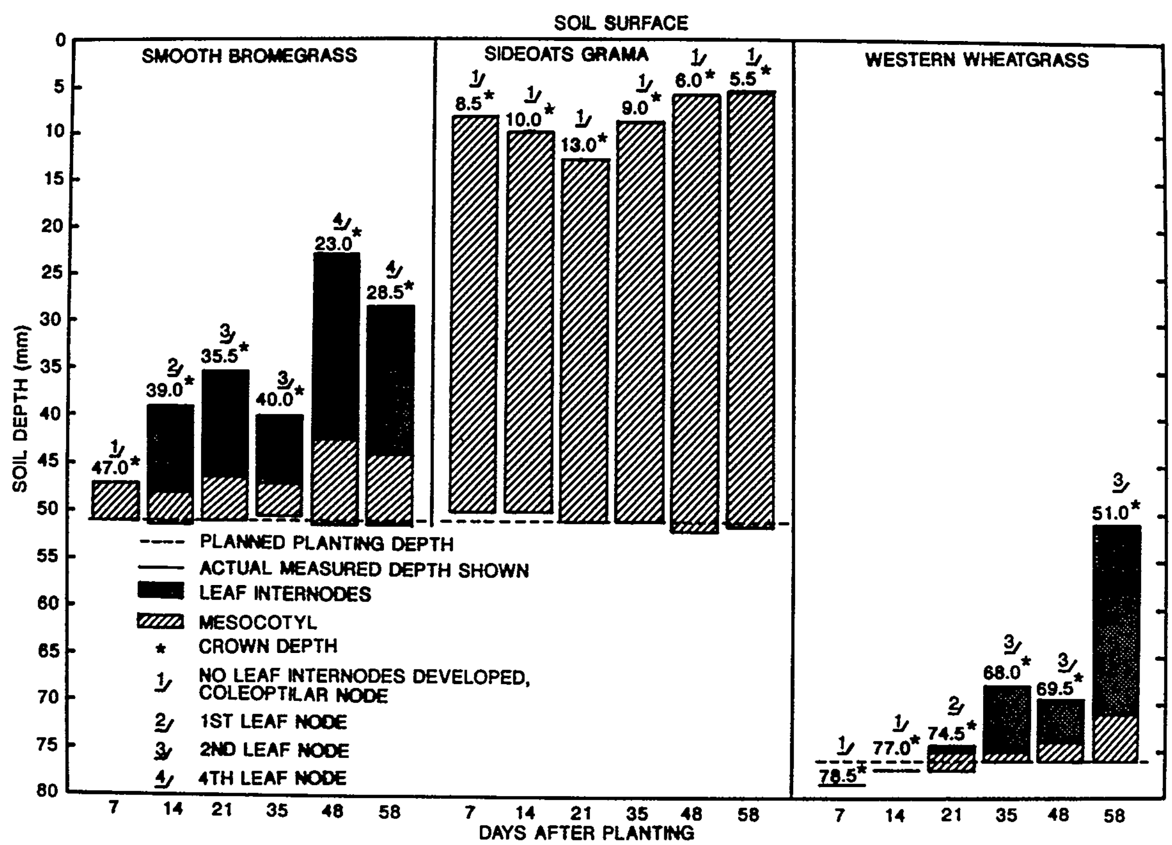

Fig. 1. Seedling crown location at various days after planting at the planting depth that maximized mesocotyl and leaf internode elongation (51 mm for smooth bromegrass and sideoats grama and 76 mm for western wheatgrass).

new seedling (Esau 1960, Hyder et al. 1971). The crown locations of establishing smooth bromegrass, sideoats grama, and western wheatgrass seedlings at each sample date of this 58-day study are shown in Fig. 1. The planting depths of 51 mm for smooth bromegrass and sideoats grama and 76 mm for western wheatgrass maximized the elongation of the mesocotyl and leaf internodes of establishing grass seedling. At 48 days after planting, the crown node for smooth bromegrass was the 4th leaf node. The crown node for sideoats grama was always at the coleoptilar node, which reached its minimum depth in the soil about 14 days after planting. Planting seeds at 76 mm resulted in crowns of western wheatgrass being located at the second leaf node 35 days after planting. Some variation in position of the crown at the 6 harvest dates would be expected since data were collected by destructive sampling techniques and different plants were observed at each sampling date. These data show that the depth and location of the crown node for these species are elevated above planting depth by elongation of the mesocotyl and/or leaf internodes. Final crown location is important to grass seedling establishment and production because most tillers and adventitious roots develop at this depth.

The morphological characteristics of smooth bromegrass in this study were altered by depth of planting. Smooth bromegrass seedlings had the longest observed mesocotyl when planted at 51.5 mm (Table 2). The 1st leaf internode of smooth bromegrass was longest at the 76.5 mm planting depth, second longest at the 51.5 mm planting depth and did not develop at the 25 and 8.5 mm planting depths. The 2nd leaf internode was longest when planted at 76.5 mm. The crown of smooth bromegrass seedlings was at the second leaf node when planted at 76.5 mm and was 37.5 mm below the soil surface. At the 51.5 mm planting depth, the 4th leaf node became the crown node for smooth bromegrass and was 25.5 mm below the soil surface. The coleoptilar node became the crown node for smooth bromegrass when planted at both 25 and 8.5 mm planting depths and was 20 and 6 mm below the soil surface, respectively. No seedlings emerged for smooth bromegrass from the 103 mm planting depth.

Mesocotyl length of the sideoats grama seedlings increased progressively with increased planting depth from 9 to 51 mm (Table 2). In all cases, the coleoptilar node was the crown node. The crown node was deepest when the seed was planted at 51 mm. The crown node was at a 2 mm depth when seed was planted at either 9 or 25.5 mm. For sideoats grama, the mesocotyl length and crown depth were increased by depth of planting. Sideoats grama seedlings did not emerge from the 76.5 or 101.5 mm planting depths.

The longest mesocotyl for western wheatgrass occurred on plants from the 76 mm planting depth, but was only 4 mm long (Table 2). The longest 1st leaf internode was 8 mm from the 76 mm planting depth. The coleoptilar node became the crown for all western wheatgrass seedlings when planted at 9, 26.5, 51, and 102 mm. The crown node was the 2nd leaf node for western wheatgrass seedlings planted at 76 mm and was elevated 14 mm above planting depth. Only 2 seedlings of western wheatgrass emerged from the 102 mm planting depth. These seedlings were weak upon emergence and showed no mesocotyl or leaf internode development (Table 2).

The total number of adventitious roots generally decreased with an increase in planting depth. However, the number of adventitious roots at the coleoptilar node were statistically the same for smooth bromegrass seedlings planted at 8.5 and 25 mm, sideoats grama planted at 9, 25.5, and 51 mm, and for western wheatgrass seedlings planted at 9, 26.5, and 51 mm (Table 3). With mesocotyl and/or leaf internode elongation, adventitious roots were distributed at different depths and at different nodes of the establishing grass seedling. The Haun leaf scale (Haun 1973), a mea-

Table 2. Grass seedling morphology altered by planting depth at final sample date.

Depth of Planting	n	Mesocotyl	Leaf Internodes[1] 1st	2nd	3rd	4th	Crown Depth[2]	Node
(mm)		Vertical Lengths (mm)					(mm)	
(Smooth Bromegrass)								
8.5[3]	6	2.5 b	0.0 c	0.0b	0.0a	0.0 a	6.0	Coleoptilar
25.0	6	5.0 ab	0.0 c	0.0 b	0.0 a	0.0 a	20.0	Coleoptilar
51.5	6	9.5 a	11.5 b	3.5 ab	0.5 a	1.0 a	25.5	4th leaf
76.5	3	6.0 ab	22.5 a	10.5 a	0.0 a	0.0 a	37.5	2nd leaf
103.0		NE[4]						
(Sideoats Grama)								
9.0	6	7.0 c	ND[5]				2.0	Coleoptilar
25.5	6	23.5 b	ND				2.0	Coleoptilar
51.0	6	46.0 a	ND				5.0	Coleoptilar
76.5		NE						
101.5		NE						
(Western Wheatgrass)								
9.0	6	0.0 b	0.0 a	0.0 a	ND		9.0	Coleoptilar
26.5	6	0.0 b	0.0 a	0.0 a	ND		26.5	Coleoptilar
51.0	6	2.0 ab	0.0 a	0.0 a	ND		49.0	Coleoptilar
76.0	6	4.0 a	8.0 a	2.0 a	ND		62.0	2nd leaf
102.0	2	0.0 b	0.0 a	0.0 a	ND		102.0	Coleoptilar

[1]Leaf internode nomenclature follows that suggested by Ries and Hoffmann (1991).
[2]Depth of crown below soil surface.
[3]All measurements rounded to nearest 0.5 mm, within columns, means followed by same letter are not different at $P \leq 0.05$ (Protected Waller/Duncan test, k=100).
[4] NE - no plants emerged from these depths.
[5] ND - no internode development.

Table 3. Nodes, depths, adventitious root numbers, Haun leaf scale, and percent emergence at final sample date.

Depth of Planting	n	Nodes[1] Coleoptilar depth[2]	Coleoptilar Adv. roots	1st Leaf depth	1st Leaf Adv. roots	2nd Leaf depth	2nd Leaf Adv. roots	3rd Leaf depth	3rd Leaf Adv. roots	4th Leaf depth	4th Leaf Adv. roots	Haun Leaves Stage[3]	Emergence
(mm)		mm	#	mm	#	mm	#	mm	#	mm	#		%
(Smooth Bromegrass)													
8.5[4]	6	6.0	15*[5]a									7.0 a	57 a
25.0	6	20.0	13* a									7.3 a	57 a
51.5	6	42.0	2 b	30.5	8 a	27.0	2 a	26.5	1	25.5	1*	5.9 a	21 b
76.5	3	70.5	1 b	48.0	2 b	37.5	4* a					3.5 b	2[6] b
103.0	---	---	---	---	---	---	NE[7]	---	---	---	---	---	0 b
(Sideoats Grama)													
9.0	6	2.0	18* a									8.3 a	72 a
25.5	6	2.0	16* a									7.5 a	50 b
51.0	6	5.0	12* a									6.1 b	7 c
76.5	---	---	---	---	---	---	NE	---	---	---	---	---	0 c
101.5	---	---	---	---	---	---	NE	---	---	---	---	---	0 c
(Western Wheatgrass)													
9.0	6	9.0	15* a									6.9 a	64 a
26.5	6	26.5	14* a									5.7 ab	60 a
51.0	6	49.0	11* a									5.5 ab	60 a
76.0	6	72.0	4 b	64.0	3	62.0	1*					4.7 b	6[6] b
102.0	2	102.0	0* b									0.6 c	1[6]b

1 Node nomenclature follows that suggested by Ries and Hofmann (1991).
2 Depth of node below soil surface.
3 Haun leaf stage (Haun, 1973).
4 All measurements rounded to nearest 0.5 mm or nearest whole root; within columns, means followed by same letter are not different at $P \leq 0.05$ (Protected Waller/Duncan test, k=100).
5 * indicates crown location.
6 % Emergence observed for all seeds planted (smooth bromegrass and western wheatgrass n=210).
7 NE - no plants emerged from these depths.

sure of seedling maturity, showed significantly slower maturity for seedlings that had to emerge from greater planting depths. Percent emergence also decreased with increased planting depths.

These data show that seedling morphological characteristics are affected by planting depth. Care must be taken in seedling evaluation studies to ensure a planting depth great enough to allow for potential elongation of the mesocotyl, coleoptile, and/or leaf internodes. Grass seedlings do not continue to elongate their mesocotyl, coleoptile, or leaf internodes, even if genetically possible, when certain soil surface temperature and light conditions are encountered. However, elongation of the mesocotyl, coleoptile, or leaf internodes does continue, if genetically possible, when these surface conditions are not encountered. This research is complicated because of the decrease in number of seedlings in any seed lot that can emerge and establish from greater planting depths.

Conclusions

The morphological characteristics of smooth bromegrass, sideoats grama, and western wheatgrass seedlings changed as depth of planting increased. These data clarify some of the conflicting results reported in the literature where mesocotyl or leaf internode elongations differed among studies. Mesocotyl, coleoptile, and/or leaf internode elongation does not occur equally at all planting depths. Within the genetic limit of individual genotype within each species, shallow planting depth decreased internode elongation while deep planting increased maximum internode elongation at the expense of emergence. When evaluating grass seedling morphology, regardless of species or seed size, planting depth must be great enough to allow for maximum genetic potential elongation of mesocotyl, coleoptile, and leaf internodes. However, when planting for a grass stand, the sower should keep in mind that percent emergence for smooth bromegrass, sideoats grama, and western wheatgrass decreased significantly when planted deeper than 26, 8, and 52 mm, respectively. Also, adventitious root numbers at the coleoptilar node decreased significantly when planting depths exceeded 25, 51, and 51 mm, respectively, for smooth bromegrass, sideoats grama, and western wheatgrass.

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