Research observations: Standardized terminology for structures resulting in emergence and crown placement of 3 perennial grasses

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Abstract

A significant problem we encountered in grass establishment research was confusion in the literature over seedling structures and terminology. From review of the historical literature and our observations of growth-chamber grown sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], western wheatgrass [*Agropyron smithii* Rydb.; new cytogenetic = *Pascopyron smithii* Rydb. (Löve)], and smooth brome grass (*Bromus inermis* Leyss.) seedlings, we suggest standard structures and terminology for grass seedlings. The nodes of a grass seedling are defined as the scutellar node, coleoptilar node, and leaf nodes named in sequence from first to last. The internode between the scutellar and coleoptilar nodes is termed the mesocotyl. The internode that develops inside the coleoptile between the coleoptilar and first leaf nodes is defined as the first leaf internode. Subsequent internodes are named for the leaf node immediately above; e.g., second leaf internode. Using these structures and terminology we found the "mechanism" of emergence for these grass seedlings from a 25-mm seeding depth was elongation of the mesocotyl (when expressed) and elongation of the coleoptile. Sideoats grama had a long mesocotyl and short coleoptile; western wheatgrass lacked or had a short mesocotyl and a long coleoptile; and smooth brome grass had intermediate mesocotyl and coleoptile lengths. The "mechanism" of crown placement for seedlings that emerged and survived from a 51-mm seeding depth was non-elongation or elongation of the mesocotyl and leaf internodes. The crowns of sideoats grama seedlings were at the coleoptilar node, which was close to the soil surface. Western wheatgrass seedlings have their crowns near planting depth, usually at the coleoptilar node. Smooth brome grass crowns were at variable depths because of variable elongation of the mesocotyl and leaf internodes.

Key Words: mesocotyl, coleoptile, leaf internodes, intracoleoptile internode, grass seedling morphology, western wheatgrass, sideoats grama, smooth brome grass

Terminology for morphological structures of developing grass seedlings remains confusing because of the historical controversy regarding the nature of the parts of the grass embryo and associated terminology (Esau 1977). A standardized terminology for grass seedling structures would improve communications and understanding of grass seedling development, better describe the location of nodes and internodes for young grass seedlings, and clearly contrast similarities and differences between grass seedlings.

This paper reviews the historical development of the terminology describing grass seedling morphology and suggests standardized structures and terminology for grass seedlings. This terminology is used to characterize the morphological development resulting in emergence and crown placement of growth-chamber grown sideoats grama, western wheatgrass, and smooth brome grass seedlings.

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Historical and Suggested Terminology

Van Tieghem (1872) was one of the first to study the structure of grasses. He proposed 3 morphological types of Gramineae (Van Tieghem 1897). Avery (1930) selected corn (*Zea mays* L.), oats (*Avena sativa* L.), and wheat (*Triticum vulgare* Vill.) seedlings for detailed study because they represented the 3 types distinguished by Van Tieghem (Fig. 1). Avery concluded, "the 3 morphological

Fig. 1. Morphological structures of 3 classical grass seedlings (after Van Tieghem 1872 and 1897, and Celakovsky 1897).

types distinguished by Van Tieghem are fundamentally 1 type, appearing different upon development because of the difference in location of the meristematic region in the first internode. . ."

Hoshikawa (1969) recognized 6 types of grass seedling based on the morphology of the underground organs and 7 types based on mode of seedling establishment. Two types of grass seedlings considered by Hyder et al. (1971) and Hyder (1974) were the Panicoid type represented by blue grama [*Bouteloua gracilis* (HBK.) Lag.] and the Festucoid type represented by crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] (Fig. 2). The deeper

Fig. 2. Seedling types considered by Hyder (after Hyder 1974).

Fig. 3. Photographs of sideoats grama, western wheatgrass, and smooth brome grass seedlings. (A = scutellar node within embryo in seed; A-B = mesocotyl; B = coleoptilar node; B-C = first leaf internode; C = first leaf node; C-D = second leaf internode; D = second leaf node; D-E = third leaf internode; and E = third leaf node). The crown for sideoats grama is at the coleoptilar node, at the second leaf node for western wheatgrass, and at the third leaf node for smooth brome grass.

location of adventitious roots in relation to seeding depth was the reason given for more successful seedling establishment of crested wheatgrass compared with blue grama.

While we can recognize the types of grass seedlings considered by Van Tieghem, Hoshikawa, and Hyder, they are similar in structural development. The primary differences among the types of seedlings are in the non-development or variable development of the first internode and the non-elongation or variable elongation of the second and subsequent internodes.

Avery (1930) also discussed the nodes of the 3 types of grasses relative to node and internode location. He considered the scutellar node, the node between the root and shoot, to be the first node, common to both the grass embryo and the grass seedling, and the coleoptilar node to the second node. The coleoptile extends above the coleoptilar node and is generally accepted as a soil penetrating sheath for the plumule common to all grasses (Brown 1965). Avery (1930) considered the first true leaf node of the grass plant to be the third node, with subsequent leaf nodes numbered in sequence. McCall (1934) also worked with oats, wheat, and corn and proposed an additional node between the scutellar and coleoptilar nodes. Our observations lead us to agree with Avery (1930) and Boyd and Avery (1936) in considering the coleoptilar node as the second node of the grass seedling. All the nodes described by Avery

(1930) are common to most cereal and forage grass seedlings. The presence and length of elongated internodes between these nodes are variable.

Celakovsky (1897), in agreement with Van Tieghem (1872), used the term mesocotyl to describe the first internode of corn and oats. He defined it as an elongated first node, belonging to neither the epicotyl nor to the hypocotyl of the grass seedling (Fig. 1). This resulted in much discussion and disagreement; but, mesocotyl gained a rather common acceptance. Avery (1930) believed the term mesocotyl, which implied that the first internode is part of the cotyledon, was meaningless, and Boyd and Avery (1936) recommended that it be dropped from the literature. Hyder et al. (1971) and Hyder (1974) accepted the recommendation of Boyd and Avery (1936) and named the first internode of blue grama the subcoleoptile internode.

Brown (1960, 1965) discussed in detail the history and terms used to describe the parts of grass embryos and seedlings. He concluded that since the mesocotyl cannot be homologous with any stem structure, the term is justified and should be retained. Since 1965, the term mesocotyl has remained in common usage as the name for the first internode in the grass seedling (Hoshikawa 1969, Harberd 1972, Vanderhoeft et al. 1979, Turner et al. 1982, and Soman et al. 1989). We concur with Brown (1960, 1965) in the use of the term mesocotyl (syn. subcoleoptile internode) as defined by Esau (1977), which is the internode between the scutellar node and the coleoptile in the embryo and seedling of Poaceae. This definition removes the implication that bothered Avery (1930) concerning the mesocotyl being part of the cotyledon.

Avery (1930) reported a variably elongated second internode for corn, oats, and wheat that is sheathed by the coleoptile while developing between the coleoptilar and first leaf nodes. Hyder et al. (1971) and Hyder (1974) termed this second internode the intracoleoptile internode. Hyder (1972) described the sequence of grass stem development as blade elongation, followed by sheath elongation, and finally internode elongation if it occurred. While this developmental sequence has some overlap, it is primarily a 1, 2, 3 sequence. We suggest that the second internode be named the first leaf internode since developmentally it is associated with the first leaf node.

Other elongated internodes of the corn, oats, and wheat seedlings were considered interleaf internodes (Avery 1930). We believe these are best named by the leaf node immediately above the internode developed. Therefore, the internode between leaf 1 and leaf 2 would be called the second leaf internode, the internode between leaf 2 and leaf 3 would be called the third leaf internode, and so on.

Onderdonk and Ketcheson (1972) reviewed the grass embryo and seedling terminology controversy and presented a numbering system for describing the structures of a corn seedling. While this system defines the number of the nodes and internodes of the corn seedling, much information is lost concerning the location and characteristics of the nodes and internodes. Secondly, this numbering system is not readily usable for other grass seedling types because the first observed elongated internode may be a mesocotyl (oats) or the first leaf internode (wheat).

Our suggested standardized terminology for the structures of the grass seedling defines the nodes as the scutellar node, coleoptilar node, and leaf nodes named in sequence from first to last (Fig. 3). The coleoptiles that once extended above the coleoptilar nodes are not referred to in Figure 3 because by this stage of seedling development they have deteriorated and essentially disappeared. The first internode between the scutellar and coleoptilar nodes is the mesocotyl. The second internode that develops inside the coleoptile between the coleoptilar and first leaf nodes is termed the first leaf internode. Other leaf internodes are named for the leaf node

immediately above; e.g., second leaf internode, third leaf internode, and so on.

Methods

A growth chamber study was conducted to evaluate the morphological development of smooth bromegrass, sideoats grama, and western wheatgrass seedlings. This study was replicated 3 times and conducted twice during the winter of 1987–88. Cone containers (38-mm top diameter, 210-mm long, 2° taper with a volume of 163,870 mm³) were painted black. Cones were packed at a bulk density of 1.4 g/cm³ with Lihen soil (sandy, mixed Entic Haploborolls) to the desired planting depth (25 and 51 mm), seeded, and packed with the same soil and at the same bulk density to 10 mm of the top. High intensity sodium and multivapor lamps produced about 876 micro moles m⁻²s⁻¹ at the plant level.

Temperatures were 24 ± 1° C during the 14-hour light period and 18 ± 1° C during the 10-hour dark period. Relative humidity was 50 ± 10% throughout the day. Nutrient levels were maintained by watering with 0.5x Hoagland's nutrient solution (100 ppm N) once each week. In the first run of the study, cones were watered daily to field capacity (18% soil water by weight) for 20 days. The emerged plants became purple and grew slowly. Watering was reduced to maintain about 10% soil water by weight. With this water level, the plants regained their green color and grew normally. For the second run, cones were watered to field capacity for 2 weeks after seeding and maintained at 10% soil water by weight for the rest of the study. Plants were normal in growth and color.

Seedlings seeded at a 25-mm depth were washed from the soil and measured 7 days after seeding to evaluate structures resulting in emergence. Seedlings seeded at a 51-mm depth were washed from the soil and measured at least 48 days after seeding to evaluate structures resulting in crown placement. Measurements included the vertical length of the mesocotyl, coleoptile, and internodes, actual depth of planting, and location of the tips of the coleoptiles. Six seedlings, 3 from each run, were averaged to reflect the vertical length of emergence structures and the vertical length of structures that resulted in the seedling crowns being placed at a certain depth in the soil.

Results

Emergence of all 3 grass species from the 25-mm seeding depth was the result of elongation of the mesocotyl (when expressed) and elongation of the coleoptile (Fig. 4). This is consistent with the findings of Avery (1930) and Boyd and Avery (1936). Sideoats

Fig. 4. Mean mesocotyl and coleoptile vertical elongation resulting in grass seedling emergence from a 25-mm seeding depth.

grama had the longest mesocotyl and shortest coleoptile, while western wheatgrass often had no or a very short mesocotyl and a long coleoptile. This is similar to the findings reported by Hyder et al. (1971) and Hyder (1974) for blue grama and crested wheatgrass. Smooth bromegrass, not considered by Hyder et al. (1971) or Hyder (1974), had intermediate mesocotyl and coleoptile lengths and was similar to the oat type seedling considered by Avery (1930).

The crown of a grass seedling is any section of stem base in which 2 or more nodes remain close together (Hyder 1974). Crown location is important because most tillers and adventitious roots develop at this depth in the soil. Generally, grass seedlings are not considered established until adventitious roots develop enough to insure an adequate water and nutrient supply to the new seedlings (Esau 1960, Hyder et al. 1971). Crown placement for sideoats grama seedlings was at the coleoptilar node for all seedlings that emerged and survived when seeded at a depth of 51 mm (Fig. 5).

Fig. 5. Mean mesocotyl vertical elongation resulting in crown placement for sideoats grama and western wheatgrass seedlings that emerged and survived from a 51-mm seeding depth.

The crown of sideoats grama seedlings observed was at an average depth of 6-mm below the soil surface. Crown placement for western wheatgrass was also most often at the coleoptilar node for seedlings that emerged and survived when seeded at a depth of 51 mm (Fig. 5). Because of the absence of short length of the mesocotyl, the crown for these western wheatgrass seedlings was near seeding depth and averaged 49.2-mm below the soil surface. However, other nodes can become the crown as is the case for the western wheatgrass seedling shown in Figure 3.

Crown placement for smooth bromegrass occurred in 3 distinct groups for the seedlings that emerged and survived when seeded at 51 mm (Fig. 6). Of the 6 individuals observed in this study, the crown developed at the first leaf node for 3 seedlings (group 1); at the second leaf node for 1 seedling (group 2); and at the fourth leaf node for the 2 remaining seedlings (group 3). Due to variable expression and elongation of the mesocotyl and leaf internodes, crown depths varied. Crown depth for the seedlings in group 1 averaged 22.5-mm below the soil surface. The seedling in group 2 had a crown 34.0-mm below the soil surface, and the crown depth for seedlings in group 3 averaged 25.5-mm below the soil surface.

Fig. 6. Mean mesocotyl and leaf internodes vertical elongation resulting in crown placement for smooth bromegrass seedlings that emerged and survived from a 51-mm seeding depth.

In smooth bromegrass seedlings, various leaf nodes became the crown rather than the coleoptilar node.

Summary

The suggested standardized terminology and structures of the grass seedling are the scutellar node, coleoptilar node, and leaf nodes named in sequence from first to last. The first internode between the scutellar and coleoptilar nodes is the mesocotyl. The second internode that develops inside the coleoptile between the coleoptilar and first leaf nodes is termed the first leaf internode. Other leaf internodes are named for the leaf node immediately above; e.g., second leaf internode, third leaf internode, and so on.

Emergence and crown placement are important to successful grass seedling establishment. The "mechanism" of emergence for grass seedlings was elongation of the mesocotyl (when expressed) and elongation of the coleoptile. The "mechanism" of crown placement for grass seedlings was non-elongation or elongation of the mesocotyl and leaf internodes. Smooth bromegrass seedlings exhibited the most variable crown placement.

- Avery, G.S., Jr. 1930. Comparative anatomy and morphology of embryos and seedlings of maize, oats, and wheat. *Bot. Gaz.* 89:1-39.
- Boyd, L., and G.S. Avery, Jr. 1936. Grass seedling anatomy: The first internodes of *Avena* and *Triticum*. *Bot. Gaz.* 97:765-779.
- Brown, W.V. 1960. The morphology of the grass embryo. *Phytomorphology* 10:215-223.
- Brown, W.V. 1965. The grass embryo—a rebuttal. *Phytomorphology* 15:274-284.
- Celakovsky, L.J. 1897. Ueber die homologien des Grasembryos. *Bot. Zeit.* 55:141-174. (cf. Avery, 1930).
- Esau, K. 1960. *Anatomy of seed plants*. 1st Ed. John Wiley & Sons, Inc., New York.
- Esau, K. 1977. *Anatomy of seed plants*. 2nd Ed. John Wiley & Sons, Inc., New York.
- Harberd, D.J. 1972. A note on the relevance of the mesocotyl in the systematics of the Gramineae. *Ann. Bot.* 36:599-603.
- Hoshikawa, K. 1969. Underground organs of the seedlings and the systematics of Gramineae. *Bot. Gaz.* 130:192-203.
- Hyder, D.N. 1972. Defoliation in relation to vegetative growth, p. 304-317. In: Younger, V.B. and C.M. McKell (eds.). *Biology and Utilization of Grasses*. Academic Press, New York.
- Hyder, D.N. 1974. Morphogenesis and management of perennial grasses in the United States, p. 89-98. In: *Plant morphogenesis as a basis for scientific management of range resources*. Proc. Workshop of the U.S./Australian Rangeland Panel (29 Mar-5 Apr 1971, Berkeley, Calif.) USDA Misc. Pub. 1271.
- Hyder, D.N., A.C. Everson, and R.E. Bement. 1971. Seedling morphology and seedling failures with blue grama. *J. Range Manage.* 24:287-292.
- McCall, M.A. 1934. Developmental anatomy and homologies in wheat. *J. Agr. Res.* 48:283-321.
- Onderdonk, J.J., and J.W. Ketcheson. 1972. A standardization of terminology for the morphological description of corn seedlings. *Can. J. Plant Sci.* 52:1003-1006.
- Soman, P., K.N. Rai, and F.R. Bidinger. 1989. Dwarfing gene effects on coleoptile length in pearl millet. *Crop Science* 29:956-958.
- Turner, F.T., C.C. Chen, and C.N. Bollich. 1982. Coleoptile and mesocotyl lengths in semidwarf rice seedlings. *Crop Science* 22:43-46.
- Vanderhoef, L.N., P.H. Quail, and W.R. Briggs. 1979. Red light-inhibited mesocotyl elongation in maize seedlings. II. Kinetic and spectral studies. *Plant Physiol.* 63:1062-1067.
- Van Tieghem, P. 1872. Observations et anatomiques sur le cotyledon des Graminées. *Ann. Sci. Nat. Bot.* V. 15:236-276. (cf. Avery, 1930).
- Van Tieghem, P. 1897. Morphologie de l'embryon et de la plantule chez les Graminées et les Cypérocees. *Ann. Sci. Nat. Bot.* VIII. 3:259-309. (cf. Avery, 1930).