Aerenchyma Development in Native Warm-Season Grass Cultivars

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Abstract

The primary objective of this study was to determine the suitability of selected warm-season grass species/cultivars for use in riparian buffers where flooding can be expected. This study focused on the development of aerenchyma in the roots of plants placed under flooding compared with non-flooding conditions. One-year old plants from 26 cultivars representing six native warm-season species (big bluestem, *Andropogon gerardii,* Vitman., 8 cultivars; little bluestem, *Schizachyrium scoparium* Michx., 1 cultivar; switchgrass, *Panicum virgatum* L., 9 cultivars; indiangrass, *Sorghastrum nutans* L., 5 cultivars; prairie cordgrass, *Spartina pectinata* L.,1 cultivar; and eastern gamagrass, *Tripsacum dactyloides* L., 2 cultivars) were transplanted into 15-cm diameter by 120-cm deep PVC pots and grown under well-drained or waterlogged conditions. After approximately 100 d, pots were opened and root samples collected for root length distribution and aerenchyma formation determinations. Aspects of aerenchyma development included percent of root cross sectional area as aerenchyma and whether the aerenchyma development was schizogenic (typical of constitutive aerenchyma) or lysigenic (characteristic of facultative aerenchyma which usually develop after stress initiation). Cultivars with limited aerenchyma development always had poor root growth into saturated soils. Conversely, cultivars with extensive aerenchyma development usually, but not always, had better than average root growth under anaerobic conditions. Suitable plant materials for inclusion in riparian buffers were found among five of the six warm-season species examined, although some species, such as eastern gamagrass, appeared to be more likely than others, such as big bluestem, to provide cultivars that were tolerant of anaerobic soils.

Introduction

Plants growing in riparian buffers are subjected to a variety of stresses due to periodic flooding of their habitat including reduced nutrient uptake, increased accumulation of potentially harmful gasses such as ethylene, and reduced oxygen availability (Visser et al., 2000). Many aquatic plant species develop aerenchyma in their roots. These large intercellular spaces allow movement of oxygen down into submerged root tissues, thus allowing continued growth and nutrient uptake. Aerenchyma may form during the ontogeny of a root through the separation of cortical cells (Esau, 1965). This form of development is called schizogenic and is typical of aquatic plants and other species that constitutively develop aerenchyma. Plants that develop aerenchyma in already formed roots in response to flooding or other environmental triggers (i.e. facultative development) do so by lysigenically breaking down the existing walls or by tearing of the cell walls (rhexigeny). Anatomically, schizogenic aerenchyma are of regular form and have smooth walls, while lysigenic or rhexigenic aerenchyma are irregular with pieces of broken walls visible (Esau, 1965). Relative to this experiment, aerenchyma have been observed in *Tripsacum* species, including eastern gamagrass (*Tripsacum dactyloides* - Clark et al. 1998; Ray et al. 1998), *Andropogon* species (*Andropogon gayanus* - Baruch and Merida, 1995); *Spartina* species (*Spartina patens* - Pezeshke, et al. 1993; *Spartina alterniflora* - Naidoo et al. 1992); and *Panicum virgatum* (Zobel, unpublished). Various studies have suggested that a positive relationship exists between the frequency of flooding experienced by a given species and the ability of that species to form aerenchyma (Visser et al. 2000). Similarly, increased aerenchyma formation is positively related to increased growth and survival under waterlogged conditions. However, anatomical features that facilitate growth in waterlogged soils may cause limitations for root function under well-drained conditions (McDonald et al., 2002).

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Native warm-season grasses are a potentially important component of riparian buffers designed to reduce nonpoint-source pollution (nutrients, pesticides, and pathogens) of eastern streams and rivers. Natural Resources Conservation Service (NRCS) personnel are often called on to provide guidance on what plant materials are suitable for various conservation applications. However, little is known about the performance of NRCS warm-season grass cultivars under saturated soil conditions. The objective of this study was to quantify differences in root production among warm-season grass cultivars in anaerobic saturated soil conditions such as those that would be commonly found along bottomlands adjacent to field streams. This information will serve to improve field office recommendations to landowners for selecting the best-suited material for saturated sites.

Material and Methods

This study included 26 warm-season grass cultivars from 6 native species. The following species and cultivars were included: 1) big bluestem (*Andropogon gerardii*, Vitman) cv. Kaw, Roundtree, OH-370, Suther, Niagara, Bison, Earl and Bonilla; 2) little bluestem (*Schizachyrium scoparium* Michx.) cv. Suther; 3) switchgrass (*Panicum virgatum* L) cv. Blackwell, Kanlow, Shelter, Hightide, Contract, Forestburg, Alamo, Cave-in-Rock and Dakota; 4) indiangrass (*Sorghastrum nutans* L.) cv. Cheyenne, Tomahawk, Osage, Suther and Rumsey; 5) prairie cordgrass (*Spartina pectinata* L.) cv. Red River; and 6) eastern gamagrass (*Tripsacum dactyloides* L.) cv. NY tetraploid and Pete. The study was conducted in a greenhouse at the NRCS Cape May Plant Materials Center, Cape May, NJ.

Breeder quality seed from each cultivar were germinated in Petri dishes then transplanted into 10 x 10 x 35 cm pots filled with a sandy soil (89.5% sand) in the early spring of 2000 and placed in a greenhouse providing a 14 h photoperiod and day/night temperatures of 27-29/16-18° C. Water content at saturation and field capacity of the soil were determined by filling 5-cm diameter by 100-cm tall clear plastic tubes with soil then placing the tubes in a water bath to a depth of 50 cm. Water uptake occurred through hole drilled in the bottoms of the tubes. After several days, the visible wetting front was measured from the water line with a ruler then water was added to the top of each tube to saturate the entire column. The soil was allowed to drain into the water bath for 24 h, then soil water content in 5-cm increments from 15 cm below to 30 cm above the water line was determined gravimetrically. Field capacity was determined to be 0.13 g g^{-1} and when fully saturated, soil moisture content was 0.17 g g^{-1}.

In May 2000, pots were relocated to a cold-frame hoop house and allowed to grow for one season. In early February 2001, dormant plants were removed from their pots and roots and shoots trimmed to 8 and 15 cm, respectively. Trimmed plants were then transplanted to 15 x 120 cm PVC pots with wire mesh bottoms. Pots were filled with the same soil as previously. Plants were again placed in a heated greenhouse with 12 replicates per cultivar. Six replicates were watered to maintain adequate soil moisture content but were allowed to drain freely, while six replicates were placed in standing water to a depth of 60 cm and also watered from above to maintain adequate surface soil water availability. On 22 May 2001, plants were harvested by laying each pot on its side and removing one-half of the PVC pot. Two-cm thick soil sections were then removed from the top, middle (at the water line), and bottom of each pot for root length density analysis. Roots were washed free of soil and root lengths measured. Two to three, 3-cm root segments were also collected just below the sections used for root length measurements and placed in FAA (formalin-acetic acid-ethanol) for aerenchyma determinations. Approximately 100 to 200 g of soil were also collected from the same area for soil moisture calculations. Root sections were embedded in paraffin and transverse sections were cut with a microtome. The presence or absence of aerenchyma and an estimate of the proportion of each transverse section containing aerenchyma was determined for roots collected from the middle section.

Results and Discussion

In the well-drained pots, soil moisture content was maintained near field-capacity near the bottom of the pot (0.12 g g^{-1}) but was quite dry at the top (0.05 g g^{-1}) despite daily irrigation applications. Extensive root development in the upper soil layer resulted in rapid water extraction and drying of the surface soil. Soil moisture content in the waterlogged pots was 0.16 g g^{-1} in the middle and 0.18 g g^{-1} near the bottom of the pots. The top layer was also wetter than in the well drained pots (0.08 g g^{-1}).

Roots from 20 of the 26 cultivars reached the bottom of the 120 cm deep pots after 3 months growth under well-watered but well-drained conditions (data not shown). Only roots from Earl and Suther big bluestem, Cave-in-Rock and Kanlow switchgrass, Rumsey indiangrass, and Red River prairie cordgrass failed to reach the bottom of the pot. In contrast, only Red River prairie cordgrass extended its roots to the bottom of the pot when the lower half of the soil was waterlogged. Of the 6 cultivars that had relatively slow root growth in well-drained soils, one (Earl) also had very poor growth under saturated conditions but two (Suther big bluestem and Red River) had some of the best growth into the saturated zone. It is clear that the ability of a cultivar to extend roots into waterlogged soils must be evaluated under waterlogged conditions and cannot be inferred from growth rates under optimal soil moisture. The relatively slow root growth of Red River prairie cordgrass and Suther big bluestem in the well-drained pots supports the observation by McDonald et al. (2002) that anatomical features that facilitate growth in waterlogged soils may cause limitations for root function under well-drained conditions.

Twenty three of the 26 cultivars could be evaluated for aerenchyma formation in saturated soils (Table 1). Two cultivars, Suther little bluestem and Bison big bluestem had no roots that extended into the saturated soil and Suther indiangrass had so few roots that we were unable to collect samples for aerenchyma determination. All cultivars evaluated were aerenchymous to some extend, although OH-370 big bluestem showed only the very beginnings of aerenchyma development in the saturated zone (≈ 1% of cortex was aerenchymous). Interestingly, all species/cultivars exhibited extensive aerenchyma formation when the pots were well-watered but allowed to drain freely (data not shown) and the overall amount of aerenchyma was similar in aerated and non-aerated soils. Miller-Goodman et al. (1997) also found that aerenchyma were present in switchgrass, big bluestem, indiangrass, and eastern gamagrass cultivars growing in well-aerated conditions but in the little bluestem cultivar they examined (cv. Aldous) aerenchyma only developed with exposure to hypoxia. In contrast, we found that the cortex of Suther little bluestem was > 75% aerenchymous in the well-drained soil.

In general, greater aerenchyma formation was associated with greater root extension into saturated soils. All cultivars with < 25% aerenchyma content in the cortex performed poorly and had little root growth into the saturated zone. Although extensive aerenchyma formation was generally associated with improved root growth under waterlogged conditions this was not always the case. Both Alamo switchgrass and Bonilla big bluestem had >75% aerenchyma yet had poor root growth. Both cultivars also had relatively slow root growth under well drained condition. Further evaluation of all cultivars is needed to determine if aerenchyma development was constitutive or facultative, and to determine if a delay in development of aerenchyma until after roots encountered waterlogged soils delayed root growth into the saturated zone.

As a group, the big bluestem cultivars tended to have relatively low aerenchyma content and poor growth into poorly aerated soils. However, Suther and Roundtree big bluestem were among the best performing cultivars. Both eastern gamagrass cultivars had extensive aerenchyma formation and better than average root growth in saturated soils. Although we only examined two eastern gamagrass cultivars, Zobel (unpublished data) has surveyed 400+ eastern gamagrass ecotypes and found little variability in aerenchyma development in this species. In this study, switchgrass results were the most variable. Hightide and Contract switchgrass had poor aerenchyma development and little root growth, Alamo had extensive aerenchyma development but poor root growth, and Shelter had extensive aerenchyma development and the greatest root length density of any cultivar examined in the middle section of the saturated pots. Other switchgrass cultivars were intermediate in root growth and aerenchyma development. Red River prairie cordgrass was the only cultivar to extend its roots to the bottom of the saturated pots. Prairie cordgrass is typically found on lower, poorly drained soils and tolerates high water tables. Unfortunately, this was the only prairie cordgrass cultivar that we evaluated but the performance of

Red River suggests that this species deserves further evaluation. Suitable plant materials for inclusion in riparian buffers can be found among many warm-season species. The five best performing cultivars in this study were from five different species. Some species, however, such as eastern gamagrass, appear to be more likely than others, such as big bluestem, to provide cultivars that are tolerant of anaerobic soils.

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Table 1. Aerenchyma formation in the cortex of roots from warm-season grasses growing in saturated soil. Roots were collected from just below the boundary layer between saturated and well-watered but unsaturated soil.

	----------Aerenchyma content of Cortex----------			
No roots[1]	< 25%	25 to 50%	50 to 75%	> 75%
Suther IG[2] (22)[3]	Kaw BB (17)	Niagara BB (13)	Osage IG (3)	Shelter SG (1)
Suther LB (24)	OH-370 BB (18)		Cheyenne IG (15)	Red River PC (2)
Bison BB (24)	Hightide SG (19)		Kanlow SG (16)	Suther BB (4)
	Earl BB (20)			NY tetraploid EG (5)
	Contract SG (23)			Blackwell SG (6)
				Roundtree BB (7)
				Pete EG (8)
				Forestburg SG (9)
				Cave-in-Rock SG (10)
				Tomahawk IG (11)
				Rumsey IG (12)
				Dacotah SG (14)
				Alamo SG (21)
				Bonilla BB (24)

1 No roots of sufficient diameter for aerenchyma determinations.

2 Species abbreviations: Big bluestem, BB; Switchgrass, SG; Indiangrass, IG; Eastern gamagrass, EG; Little bluestem, LB; Prairie cordgrass, PC.

3 Values in parentheses are relative rankings for root length density at the saturated boundary layer.