Preliminary Observations on Physiological Responses of Three Turfgrass Species to Traffic Stress

Lie-Bao Han^{1,4}, Gui-Long Song^{1,4}, and Xunzhong Zhang^{2,3}

ADDITIONAL INDEX WORDS. antioxidant, electrolyte leakage, kentucky bluegrass, peroxidase, tall fescue, wear, zoysiagrass

SUMMARY. Traffic stress causes turfgrass injury and soil compaction but the underlying physiological mechanisms are not well documented. The objectives of this study were to investigate the physiological responses of kentucky bluegrass (*Poa pratensis*), tall fescue (*Festuca arundinacea*), and japanese zoysiagrass (*Zoysia japonica*) to three levels of traffic stress during the growing season under simulated soccer traffic conditions. Relative leaf water content (LWC), shoot density, leaf chlorophyll concentration (LCC), membrane permeability, and leaf antioxidant peroxidase (POD) activity were measured once per month. The traffic stress treatments caused a reduction in LWC, shoot density, LCC, and POD activity, and an increase in cell membrane permeability in all three species. Japanese zoysiagrass had less electrolyte leakage, and higher POD activity and shoot density than both kentucky bluegrass and tall fescue. The results suggest that turfgrass tolerance to traffic stress may be related to leaf antioxidant activity. Turfgrass species or cultivars with higher leaf antioxidant activity may be more tolerant to traffic stress than those with lower antioxidant activity.

Kentucky bluegrass, tall fescue, and japanese zoysiagrass are commonly used for sports and recreational areas. Turfgrasses used for recreational areas are frequently subjected to traffic stress (Bonos et al., 2001; Li and Hunt, 1997; Minner and Valverde, 2005). The term traffic stress generally includes both wear and soil compaction (Beard, 1973; Carrow and Petrovic, 1992). Soil compaction may result in poor soil physical properties, and inhibits turfgrass root growth and visual quality (Trenholm et al., 2000; Turgeon, 2005). Wear causes a direct injury to plant tissues by pressure, scuffing, abrasion, and tearing (Beard, 2005; Bonos et al., 2001; Carrow and Petrovic, 1992). Wear injury results from the weight and motion of traffic crushing and tearing the leaves, stems, and crowns of the turfgrass plant (Carrow and Petrovic, 1992; Shearman and Beard, 1975a, b; Trenholm et al., 2000).

It has been reported that warm-season turfgrass species have more tolerance to wear than cool-season species (Shearman and Beard, 1975a, b). Among warm-season turfgrass species, japanese zoysiagrass and bermudagrass (*Cynodon dactylon*) are the species with more wear tolerance (Turgeon, 2005). Among cool-season species, tall fescue, kentucky bluegrass, and perennial ryegrass (*Lolium perenne*) are considered to have relatively more wear tolerance (Minner and Valverde, 2005). However, the underlying physiological mechanisms for the difference in wear tolerance

between species are poorly understood. Relative wear tolerance of different species has varied among different studies (Canaway, 1981; Carrow and Petrovic, 1992; Minner and Valverde, 2005; Shearman and Beard, 1975a).

Turf cover, visual quality, and shoot density have been commonly used to evaluate wear tolerance (Canaway, 1981; Shearman and Beard, 1975a). Bourgoin et al. (1985) investigated plant characteristics that correlated to wear tolerance and found that high initial tillers per unit area are related to wear tolerance in tall fescue, kentucky bluegrass, and perennial ryegrass. Within perennial ryegrass cultivars, higher leaf water content (LWC) and higher acid detergent fiber (lignin and cellulose) shoot tissue content tended to be related to wear tolerance. Trenholm et al. (2000) indicated that bermudagrass wear tolerance was most strongly correlated with increased stem moisture content and stem cellulose content.

It has been well documented that antioxidant defense mechanisms are involved in plant tolerance to stresses (Inze and Montagu, 2002). Various abiotic and biotic stresses may reduce photosynthetic rates. Chloroplasts may be exposed to excess excitation energy, especially under high light (Inze and Montagu, 2002). Electrons leaked from electron transport chains in the chloroplasts can react with O₂ to produce reactive oxygen species (ROS) such as hydrogen peroxide (H₂O₂). The excess ROS may cause damage to

The authors gratefully acknowledge the funding from Project of Excellent Talent in New Century of China.

¹Key Laboratory for Silviculture and Conservation of Ministry of Education, Institute of Turfgrass Science, Beijing Forestry University, Beijing, China 100083

²Department of Crop and Soil Environmental Sciences, Virginia Tech, Blacksburg, VA 24061-0404

³Corresponding author. E-mail: xuzhang@vt.edu

⁴Both authors have contributed equally to this paper.

Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29,574	fl oz	μL	3.3814 × 10 ⁻⁵
29.5735	fl oz	mL	0.0338
0.3048	ft	m	3.2808
2.54	inch(es)	cm	0.3937
25.4	inch(es)	mm	0.0394
6.4516	inch ²	cm ²	0.1550
0.4536	lb	kg	2.2046
4.4482	lbf	N	0.2248
1	meq/100 g	cmol·kg ⁻¹	1
28.3495	oz	G	0.0353
28,350	oz	mg	3.5274 × 10 ⁻⁵
305.1517	oz/ft ²	g·m ⁻²	0.0033
0.001	ppm	g·kg ⁻¹	1000
0.001	ppm	mg·g ⁻¹	1000
1	ppm	mg·kg ⁻¹	1
0.0703	psi	kg·cm ⁻²	14.2233
(°F - 32) ÷ 1.8	°F	°C	(1.8 × °C) + 32

the cell membrane through lipid peroxidation, proteins, and nucleic acids. Plants have various antioxidant metabolites and enzymes to cope with the ROS. Peroxidase (POD) is an antioxidant enzyme that can scavenge H_2O_2 . Research has shown that H_2O_2 and POD are involved in cell wall stiffening during plant hypersensitive reactions against pathogen attack (Bestwick et al., 1997; Schopfer, 1996). Stiffened cell walls have less flexibility and may be more susceptible to wear injury. However, few studies have been reported responses of antioxidant enzymes (e.g., POD) to traffic stress. Little information is available regarding physiological responses to traffic stress in cool-season and warm-season turfgrass species. This study was conducted to determine the physiological responses of three turfgrass species to different levels of traffic stress, and to investigate whether antioxidant defense is involved in traffic stress tolerance of turfgrasses.

Materials and methods

SEEDBED PREPARATION AND PLANT CULTURE. ‘Opal’ kentucky bluegrass, ‘Barlexas’ tall fescue, and ‘Common’ japanese zoysiagrass were used in this study. The seedbed construction was designed and prepared according to the U.S. Golf Association construction standard (Beard, 2005). The soil was sandy loam with good drainage. The soil volume weight was 2.87, pH was 8.43, organic matter content was 1.91%, cation exchange capacity was 3.88 $cmol\cdot kg^{-1}$, total N was 0.33 $g\cdot kg^{-1}$, available P was 5.2 $mg\cdot kg^{-1}$, and available K was 67.2 $mg\cdot kg^{-1}$. The three turfgrass species were established from seeds, with seeding rates of 30 $g\cdot m^{-2}$ (tall fescue), 10 $g\cdot m^{-2}$ (kentucky bluegrass), and 15 $g\cdot m^{-2}$ (japanese zoysiagrass) on 20 Apr. 2002. After planting, the plots (2 × 2 m) were irrigated to maintain soil moisture at 80% field capacity or higher. The turfgrasses were mowed with a rotary mower twice weekly at 4.0 cm and the clippings were removed. Fertilizer (34N-7.4P-14.1K) was applied at 10 $g\cdot m^{-2}$ once per month from July through October. Weeds were removed by hand. Fungicides were applied in June, July, and August as a curative control for

summer patch in kentucky bluegrass and tall fescue.

TRAFFIC STRESS TREATMENT. A traffic simulator, developed by the Turfgrass Research Institute at Beijing Forestry University (Beijing, China), was used to apply traffic stress on the field plots. This traffic simulator was designed to simulate traffic stress applied by a running soccer player, weighing 90 kg and wearing a pair of soccer boots with seven 9-mm-long cleats (Li and Hunt, 1997). The simulator creates a vertical pressure of 39 $kg\cdot cm^{-2}$ to the turf and a horizontal tearing force of 1055 N (Ji and Li, 1982). The traffic stress treatments included control (no traffic treatment), light traffic (every 2 weeks), moderate traffic (once per week), and heavy traffic (two traffic passes per week). The traffic treatments were initiated on 7 Aug. 2002 and finished on 8 Nov. 2002, using the reconstructed traffic simulator based on the tamping machine as described previously.

MEASUREMENTS. Two weeks after initiation of traffic stress, leaf samples were collected from each plot once per month for 3 months (August, September, and October) for analysis of LWC, leaf chlorophyll concentration (LCC), electrolyte leakage (EL), and POD activity. At the same time, three plugs (7 cm in diameter) were sampled from each plot, and the number of shoots per plug was recorded. Turfgrass shoot density was expressed as an average of shoot numbers per square centimeter.

LEAF WATER CONTENT. Fresh leaves (300 mg) were sampled randomly from each plot, weighed [fresh weight (W_f)], and placed in a Petri dish filled with distilled water for 4 h. The leaves were weighed [turgor weight or saturated weight (W_t)] after excess moisture on the leaf surface was removed with tissue paper (Gonzalez and Gonzalez-Vilar, 2001). The leaves were then dried at 80 °C for 24 h and weighed [dry weight (W_d)]. The leaf LWC was calculated as follows:

$$LWC = \frac{W_f - W_d}{W_t - W_d} \times 100$$

LEAF CHLOROPHYLL CONCENTRATION. Fresh leaves (300 mg) were randomly collected from each plot, and chlorophyll was extracted

with 80% acetone. Absorbance of extracts was measured at 645- and 663-nm wavelengths on an ultraviolet-prismatic photometer (UV7504C; Shibo BioTechnologies Co., Ltd, Shanghai, China). The LCC was expressed as milligrams chlorophyll per gram W_f (Li, 2000).

MEMBRANE PERMEABILITY. Membrane permeability (MP) was determined based on leaf EL (measured as a percentage). The greater the EL value, the higher the MP (Zhang et al., 2006). Fresh leaf blades (300 mg) were sampled from each plot and were placed in a test tube filled with 30 mL distilled water. After shaking for 12 h, the electrical conductivity (E_1) was measured with a conductivity meter (DDSJ-308A; Shanghai REX Instrument Factory, Shanghai, China). The samples were then placed in boiling water for 1 h and electrical conductivity (E_2) was measured again after the samples cooled to room temperature. The EL was calculated according to the following formula:

$$EL = \frac{E_1 - E_0}{E_2 - E_0} \times 100$$

where E_0 is the electrical conductivity of distilled water (Li, 2000).

LEAF PEROXIDE ACTIVITY. The POD activity was determined by measuring the increase in absorbance at 470 nm according to the procedure outlined by Liu and Zhang (1994). Briefly, leaf samples (250 mg) were homogenized with a pestle in an ice-cold mortar in 4 mL 50 mM sodium phosphate buffer (pH, 7.0) containing 0.2 mM ethylenediamine tetraacetic acid and 1% (w/v) polyvinylpyrrolidone. The homogenate was filtered through four layers of cheesecloth and then centrifuged at 4 °C for 20 min at 14,000 g_n . The supernatant (0.8 mL) was collected and used for POD assay. The assay contained 50 μ L 20 mM guaiacol, 2.83 mL 10 mM phosphate buffer (pH, 7.0), and 50 μ L enzyme extract. The reaction was started with 20 μ L 40 mM H_2O_2 . The oxidation of guaiacol was measured by following the increase in absorbance at 470 nm for 2 min. One unit of POD was defined as the amount of enzyme that caused a 0.01 increase in absorbance at 470 nm/min under the assay condition.

EXPERIMENTAL DESIGN AND DATA ANALYSIS. A complete randomized block design was used with three

turfgrass species and four levels of traffic stress treatments. The treatments were replicated four times. Because there were no significant interactions of traffic stress and species with the sampling dates (August, September, and October), the data from the three sampling dates were pooled and the averages were used for statistical analysis to compare the species and the levels of the traffic stress. The data were analyzed with an analysis of variance, and mean separations were performed with a Fisher's protected LSD at 5% probability levels using SPSS (version 10; SPSS, Chicago).

Results and discussions

LEAF WATER CONTENT. Traffic stress reduced LWC significantly in all three species (Table 1). As the traffic stress levels increased, the LWC decreased gradually in all three species. The heavy traffic stress (two passes per week) reduced the LWC by 9.4% in kentucky bluegrass, 8.4% in tall fescue, and 7.6% in japanese zoysiagrass when compared with the control of the same species (Table 1).

The LWC was similar among the species when they were subjected to heavy traffic stress, although differences in LWC were found between japanese zoysiagrass and kentucky bluegrass under light and moderate stress levels. The LWC reduction associated with traffic stress may be attributed to leaf injury (Beard, 2005). Traffic stress may add horizontal and vertical forces to the turf surface. Horizontal forces cause tearing of the grass and soil smearing, whereas vertical forces crush the turf against and into the soil, and cause soil compaction (Canaway, 1981). The traffic simulator used in this study applied both horizontal and vertical forces on the turf surface and may have caused leaf injury and soil compaction. The LWC reduction associated with traffic stress may be attributed to evaporation from wounds and transpiration as well as reduction in water uptake from compacted soil.

The relationship between LWC and wear tolerance was not consistent in past studies (Beard, 1973). Higher leaf moisture was associated with greater wear tolerance in warm-season species (Beard, 1973; Trenholm

et al., 2000), but not in cool-season species (Beard, 1973). The results of this study suggest that relative changes in the LWC for each species resulting from traffic stress may be more closely associated with wear tolerance than absolute LWC values because the initial LWC (before traffic stress) may differ between species.

SHOOT DENSITY. The turfgrass shoot density was significantly reduced because of traffic stress in all three species (Table 2). All levels of traffic stress caused decline of shoot density in tall fescue, and only heavy traffic stress reduced the shoot density in japanese zoysiagrass. Regardless of traffic stress levels, japanese zoysiagrass had greater shoot density relative to kentucky bluegrass and tall fescue. The shoot density decline may result from reduction in growth and death of mature shoots. Japanese zoysiagrass had higher LCC and may have more carbohydrate synthesis for growth when compared with tall fescue and kentucky bluegrass.

LEAF CHLOROPHYLL CONCENTRATION. The traffic stress reduced concentrations of chlorophyll a and chlorophyll a + b in all three turfgrass species, but did not impact chlorophyll b in japanese zoysiagrass and kentucky bluegrass (Table 3). As traffic stress levels increased, LCC declined. The moderate and heavy traffic stresses

reduced LCC in all three species. Japanese zoysiagrass had more chlorophyll a than kentucky bluegrass and tall fescue under all three levels of traffic stress (Table 3).

MEMBRANE PERMEABILITY. Traffic stress increased MP or EL in all three turfgrass species (Table 4). The heavy traffic stress increased EL by 151% in kentucky bluegrass, 196% in tall fescue, and 178% in japanese zoysiagrass when compared with the control of the same species. The EL was increased significantly in tall fescue compared with kentucky bluegrass and japanese zoysiagrass under all levels of traffic stress (Table 2). Under the heavy traffic, japanese zoysiagrass had less EL than tall fescue and kentucky bluegrass.

Membrane permeability is closely associated with cell membrane composition and physiological status (Nilsen and Orcutt, 1996). Increased EL may be partially the result of cell membrane damage by ROS, especially under the heavy traffic stress. The ROS may damage cell membrane via lipid peroxidation and has an additive effect on EL. The difference in EL between the species may be associated with antioxidant activity (Zhang et al., 2006) and leaf structure as well as cell wall composition (Trenholm et al., 2000).

PEROXIDASE ACTIVITY. The POD activity decreased as traffic stress levels

Table 1. Leaf water content of three turfgrass species under different levels of traffic stress.

Treatment	Leaf water content (%)		
	Kentucky bluegrass	Tall fescue	Japanese zoysiagrass
Control	98.2 aA ^z	96.0 aB	95.7 aB
Light traffic	97.2 bA	95.3 abAB	94.8 abB
Moderate traffic	92.8 cA	92.6 cAB	91.5 cB
Heavy traffic	88.9 dA	87.6 dA	88.1 dA

^zValues with the same lowercase letter in the same list are nonsignificant at $P = 0.05$ between traffic treatments. Values with the same uppercase letter in the same row are nonsignificant at $P = 0.05$ between species.

Table 2. Turfgrass shoot density of three turfgrass species under different levels of traffic stress

Treatment	Shoot density (no./cm ²) ^z		
	Kentucky bluegrass	Tall fescue	Japanese zoysiagrass
Control	4.5 aA ^y	4.5 aA	4.5 bA
Light traffic	5.0 bA	3.5 bB	5.0 aA
Moderate traffic	4.0 cB	2.5 cC	5.0 aA
Heavy traffic	2.0 dB	1.0d dC	3.0 cA

^z1 shoot/cm² = 6.4516 shoots/inch².

^yValues with the same lowercase letter in the same list are nonsignificant at $P = 0.05$ between traffic treatments. Values with the same uppercase letter in the same row are nonsignificant at $P = 0.05$ between species.

increased, especially for tall fescue and japanese zoysiagrass. The POD activity was the highest in japanese zoysiagrass and the lowest in kentucky bluegrass at all traffic stress levels (Fig. 1). Peroxidase, an important antioxidant enzyme, may scavenge H_2O_2 and prevent stiffening of the cell walls, and thus increase wear tolerance of leaf blades (Bestwick et al., 1997; Inze and Montagu, 2002; Schopfer, 1996). Japanese zoysiagrass with more POD activity may suppress ROS more effectively than tall fescue and kentucky bluegrass. As a result, japanese zoysiagrass may have less cell wall stiffening, allowing the cell wall to maintain more flexibility. Several studies have indicated that wear tolerance was negatively correlated with leaf total cell wall content (Canaway, 1981; Trenholm et al., 2000).

Leaf tissues and chlorophyll damaged because of traffic stress may experience oxidative stress, especially under high light conditions (Inze and Montagu, 2002). The ROS accumulation under oxidative stress may cause chlorophyll damage (bleaching) and reduce LCC. Leaf antioxidants may scavenge ROS and reduce/prevent chlorophyll damage. This is supported by the fact that japanese zoysiagrass with more POD activity had a higher LCC when compared with tall fescue and kentucky bluegrass. This suggests that turfgrass species with higher antioxidant activity may have more traffic stress tolerance than those with less antioxidant activity. Future research is needed to examine relationships of antioxidant activity with cell wall stiffening and wear tolerance.

Conclusion

The results of this study show that traffic stress greatly reduced LWC, shoot density, and LCC, and increased EL in all three turfgrass species, resulting in increased ROS damage. The plant recovery was greatly limited. As traffic stress levels increased, POD activity decreased and ROS damage to cells increased, causing an increase in EL. Japanese zoysiagrass had more tolerance to traffic stress than kentucky bluegrass and tall fescue. More traffic stress tolerance in japanese zoysiagrass was associated with more POD activity, less EL, and higher shoot density.

Table 3. Leaf chlorophyll concentration of three turfgrass species under different levels of traffic stress

Traffic treatment	Kentucky bluegrass	Tall fescue	Japanese zoysiagrass
Chlorophyll a concn ($mg \cdot g^{-1}$ FW) ^z			
Control	2.01 aA ^y	2.04 aA	2.11 aA
Light traffic	1.91 abB	1.51 bC	2.08 aA
Moderate traffic	1.80 bB	1.50 bcC	1.93 bA
Heavy traffic	1.69 cB	1.44 cC	1.76 cA
Chlorophyll b concn ($mg \cdot g^{-1}$ FW)			
Control	0.69 aA	0.63 aB	0.64 aB
Light traffic	0.65 aA	0.59 bB	0.66 aA
Moderate traffic	0.66 aA	0.53 bB	0.66 aA
Heavy traffic	0.67 aA	0.52 bB	0.67 aA
Chlorophyll a + b concn ($mg \cdot g^{-1}$ FW)			
Control	2.70 aA	2.67 aA	2.73 aA
Light traffic	2.56 abAB	2.11 bB	2.64 aA
Moderate traffic	2.46 abAB	2.03 bB	2.59 abA
Heavy traffic	2.36 bA	1.96 bB	2.42 bA

^z1 $mg \cdot g^{-1}$ = 1000 ppm.

^yValues followed by the same letters within the same column or the same uppercase letters within each row for each data set are nonsignificant at $P = 0.05$.

Table 4. Leaf electrolyte leakage of three turfgrass species under different levels of traffic stress

Treatment	Leaf electrolyte leakage (%)		
	Kentucky bluegrass	Tall fescue	Japanese zoysiagrass
Control	6.38 aA ^z	6.63 aA	5.10 aB
Light traffic	12.07 bB	16.24 bA	11.31 bB
Moderate traffic	13.27 cB	17.86 cA	12.41 bcB
Heavy traffic	16.07 dB	19.64 dA	14.20 dC

^zValues with the same lowercase letter in the same list are nonsignificant different at $P = 0.05$ between traffic treatments. Values with the same uppercase letter in the same row are nonsignificant at $P = 0.05$ between species.

Fig. 1. Response of leaf peroxidase (POD) activity of three turfgrass species to different traffic stress treatments. Vertical bars represent LSD at $P = 0.05$. FW, fresh weight. 1 unit/mg = 28,350 units/oz.

The results suggest that antioxidant defense may be involved in turfgrass tolerance to traffic stress. Selection and use of species with more antioxidant activity may be an effective approach to improve traffic stress tolerance of turfgrasses.

Literature cited

- Beard, J.B. 1973. Turfgrass: Science and culture. Prentice-Hall, Englewood Cliffs, NJ.
- Beard, J.B. 2005. Turfgrass management for golf course. 2nd ed. Sleeping Bear Press, Chelsea, MI.
- Bestwick, C.S., I.R. Beown, M.H.R. Bennett, and J.W. Mansfield. 1997. Localization of hydrogen peroxide accumulation during the hypersensitive reaction of lettuce cells to *Pseudomonas syringae* pv *phaseolicola*. Plant Cell 9: 209–221.
- Bonos, S.A., J. Watkins, J.A. Honig, M. Sosa, T. Molnar, J.A. Murphy, and W.A. Meyer. 2001. Breeding cool season turfgrasses for wear tolerance using a wear simulator. Intl. Turfgrass Soc. Res. J. 9: 137–145.
- Bourgoin, B., P. Mansat, B. AitTaleb, and M.H. Quaggag. 1985. Explicative characteristics of treading tolerance in *Festuca rubra*, *Lolium perenne*, and *Poa pratensis*, p. 235–242. In: F. Lemaire (ed.). Proc. 5th Intl. Turfgrass Res. Conf., Avignon, France. INRA, Paris.
- Canaway, P.W. 1981. Wear tolerance of turfgrass species. J. Sports Turf Res. Inst. 57:65–83.
- Carrow, R.N. and A.M. Petrovic. 1992. Effects of traffic on turfgrass, p. 285–330. In: D.V. Waddington, R.N. Carrow, and R.C. Shearman (eds.). Turfgrass. Monograph no. 32. Amer. Soc. Agron., Madison, WI.
- Gonzalez, L. and M. Gonzalez-Vilar. 2001. Determination of relative water content, p. 207–212. In: M.J. Reigosa Roger (ed.). Handbook of plant ecophysiology techniques. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Inze, D. and M.V. Montagu. 2002. Oxidative stress in plants. Taylor & Francis, New York.
- Ji, Z. and J. Li. 1982. Sports biomechanics. People's Physical Education Press, Beijing, China.
- Li, D.Y. and W.F. Hunt. 1997. Soccer wear simulation on sports turf mixture. Trans. Chinese Soc. Agr. Eng. 13:164–168.
- Li, H.S. 2000. Experiment theory and technology of plant physiology. High Education Publishing School, Beijing, China.
- Liu, Z. and S.C. Zhang. 1994. Plant stress physiology. Agricultural Press of China, Beijing, China.
- Minner, D.D. and F.J. Valverde. 2005. The effect of traffic intensity and periodicity on *Poa pratensis* L. performance. Intl. Turfgrass Soc. Res. J. 10:387–392.
- Nilsen, E.T. and D.M. Orcutt. 1996. The physiology of plants under stress. Wiley, New York.
- Schopfer, P. 1996. Hydrogen peroxide-mediated cell-wall stiffening in vitro in maize coleoptiles. Planta 99:43–49.
- Shearman, R.C. and J.B. Beard. 1975a. Turfgrass wear tolerance mechanisms: Wear tolerance of seven turfgrass species and quantitative methods for determining turfgrass wear injury. Agron. J. 67:208–211.
- Shearman, R.C. and J.B. Beard. 1975b. Turfgrass wear tolerance mechanisms: I. Effects of cell wall constituents on turfgrass wear tolerance. Agron. J. 67:212–215.
- Trenholm, L.E., R.N. Carrow, and R.R. Duncan. 2000. Mechanism of wear tolerance in seashore paspalum and bermudagrass. Crop Sci. 40:1350–1357.
- Turgeon, A.J. 2005. Turfgrass management. 6th ed. Prentice Hall, Upper Saddle River, NJ.
- Zhang, X., E.H. Ervin, and A.J. LaBranche. 2006. Metabolic defense response of seeded bermudagrass during acclimation to freezing stress. Crop Sci. 46:2598–2605.