Water Relations and Drought Tolerance of Four Turfgrasses

Yaling Qian[1] and Jack D. Fry[2]
Department of Horticulture, Forestry and Recreation Resources, Kansas State University, 2021 Throckmorton Hall, Manhattan, Kansas 66506-5506

ADDITIONAL INDEX WORDS. leaf water potential, osmotic potential, osmotic adjustment, pressure potential, *Buchloe dactyloides*, *Cynodon dactylon* x *C. transvaalensis*, *Zoysia japonica*, *Festuca arundinacea*

ABSTRACT. Greenhouse studies were conducted on three warm-season turfgrasses, 'Midlawn' bermudagrass [*Cynodon dactylon* (L.) Pers. x *C. transvaalensis* Burtt-Davy], 'Prairie' buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], and 'Meyer' zoysiagrass (*Zoysia japonica* Steud.), and a cool-season turfgrass, 'Mustang' tall fescue (*Festuca arundinacea* Schreb.) to determine 1) water relations and drought tolerance characteristics by subjecting container-grown grasses to drought and 2) potential relationships between osmotic adjustment (OA) and turf recovery after severe drought. Tall fescue was clipped at 6.3 cm once weekly, whereas warm-season grasses were clipped at 4.5 cm twice weekly. The threshold volumetric soil water content (SWC) at which a sharp decline in leaf water potential (ψ_L) occurred was higher for tall fescue than for warm-season grasses. Buffalograss exhibited the lowest and tall fescue exhibited the highest reduction in leaf pressure potential (ψ_P) per unit decline in ψ_L during dry down. Ranking of grasses for magnitude of OA was buffalograss (0.84 MPa) = zoysiagrass (0.77 MPa) > bermudagrass (0.60 MPa) > tall fescue (0.34 MPa). Grass coverage 2 weeks after irrigation was resumed was correlated positively with magnitude of OA ($r = 0.66$, $P < 0.05$).

Over the last 2 decades, turfgrass researchers have put significant effort into developing and evaluating turf species that have good drought resistance (Aronson et al., 1987; Fry and Butler, 1989; Gibeault et al., 1985). As water conservation becomes an important issue, interest is increasing in identifying grasses that require less water.

According to Levitt (1980), plants with good drought resistance are those that are able to survive stress by means of drought avoidance, drought tolerance at low leaf water potentials (ψ_L), or both. Drought-avoidance mechanisms in turf include deep and extensive rooting to maximize water absorption and shoot characteristics that minimize transpiration (Youngner, 1985). Some grasses tolerate drought by osmotic adjustment (OA), defined as the accumulation of solutes in plant tissue in response to dehydration (Turner and Jones, 1980). Osmotic adjustment can result in turgor maintenance, thereby sustaining cell elongation and leaf expansion as water deficits develop. Morgan (1983) suggested that OA measurements be used to select drought-tolerant wheat cultivars. Yield differences between two sorghum cultivars were correlated with differences in OA in greenhouse and field studies (Wright et al., 1983). Tall fescue genotypes differed in turgor maintenance as soil moisture decreased (White et al., 1992). Low leaf osmotic potential (ψ_S) before stress and OA contributed to turgor maintenance and were correlated with tiller survival of tall fescue.

In earlier work, we reported that evapotranspiration (ET) of 'Mustang' tall fescue was 19%, 34%, and 35% higher than for 'Meyer' zoysiagrass, 'Prairie' buffalograss, and 'Midlawn' bermudagrass, respectively (Qian et al., 1996b). However, tall fescue possessed 39% to 140% greater total root length than warm-season grasses in the field (Qian et al., 1996a). Zoysiagrass had an

intermediate ET rate and exhibited the lowest root length density at depths of 30 to 60 and 60 to 90 cm of the four grasses in the field. Bermudagrass and buffalograss exhibited low ET rates (Qian et al., 1996b) and relatively deep rooting (Qian et al., 1996a). Information is needed concerning the ability of these grasses to tolerate internal water deficits. Hence, the objectives of this research were to 1) provide information on the water relations and drought-tolerance characteristics of 'Midlawn' bermudagrass, 'Prairie' buffalograss, 'Meyer' zoysiagrass, and 'Mustang' tall fescue and 2) investigate potential relationships between OA and grass survival after severe drought.

Materials and Methods

This experiment was conducted from September 1994 to April 1995 and was repeated from February to July 1995 with a new set of plants. 'Prairie' buffalograss, 'Midlawn' bermudagrass, 'Meyer' zoysiagrass, and 'Mustang' tall fescue sods were collected from 3-year-old field plots. Turfs were sodded individually on a loam soil retained in PVC containers (experimental units) measuring 23 cm in diameter × 27 cm deep. Soil was a loam (22.5% sand, 48% silt, 29.5% clay, 2.9% organic matter, pH 6.5) with a bulk density of 1.45 g·cm⁻³. Greenhouse air temperature was maintained between 22 and 28 °C. Two high-intensity sodium lamps were on between 0600 to 2000 HR and were placed 170 cm above the turf canopy to supplement natural light. Greenhouse photosynthetically active radiation ranged from 900 μmol·m⁻²·s⁻¹ on a cloudy day to 1150 μmol·m⁻²·s⁻¹ on sunny day. A 20N–4P–17K soluble fertilizer was applied to provide a 2.5 g N/m² in two applications. Tall fescue was clipped once weekly at 6.3 cm, and warm-season turfgrasses were clipped at 4.4 cm twice weekly.

All grasses were maintained under well-watered conditions for >3 months before irrigation ceased. During this period, data were collected on clipping mass, shoot extension rate, and leaf water content. Clipping fresh mass was determined by collecting clippings after mowing and then weighing immediately. Dry mass was measured after clippings were dried at 80 °C for 24 h. Shoot extension rate was determined by measuring the distance between the soil surface and the top of the turf canopy before each mowing, and the mean height of three subsamples for each experimental unit was recorded.
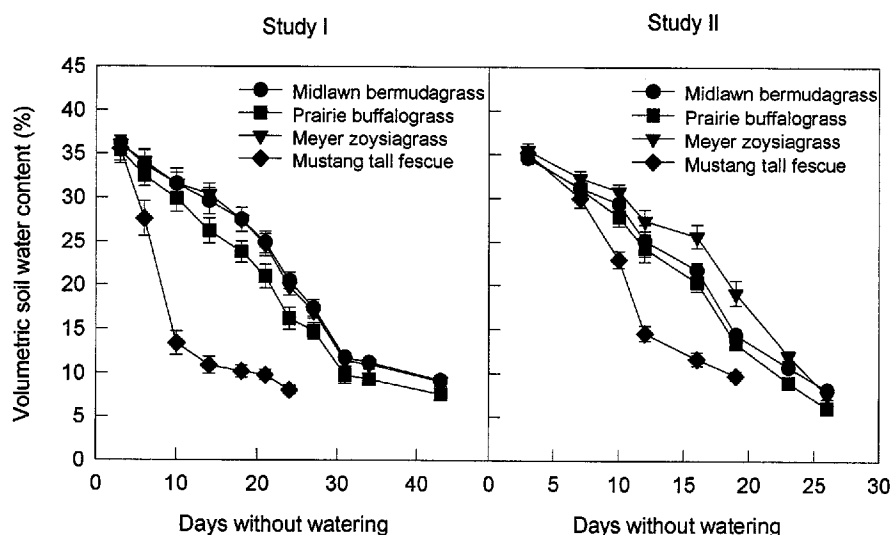
Study I / Study II

Fig. 1. Decline in volumetric soil water content under four turfgrasses after watering ceased. Each point represents the mean of four replications. Bars indicate SE.

Leaf water content (%) was calculated on fresh mass basis [(clipping fresh mass − clipping dry mass)/clipping fresh mass] × 100.

After ≈3 months under well-watered conditions, drought stress was imposed on grasses by withholding water until volumetric soil water content (SWC) reached ≈8% (25 to 45 d, depending on species). Volumetric soil water content was measured using a time domain reflectometer (TDR, IRAMS soil moisture analyzer; Soil Moisture Equipment Corp., Santa Barbara, Calif.).

During dry down, data were collected every 3 d on grass ET, ψ_L, ψ_S, and SWC. Visual observations of turf response to progressive dry down also were recorded. When the study was repeated, tall fescue response to drought was measured every 1 or 2 d.

Evapotranspiration was measured gravimetrically using a precision electronic balance (Sartorius, GMBH GOTTINGEN, Ger-

many) with accuracy to the nearest gram. Leaf water potential was measured using pre-calibrated thermocouple psychrometers (model 75-1 AC; J.R.D. Merrill Specialty Equipment Corp., Logan, Utah) and a dewpoint microvoltmeter (model HR-33T; Wescor, Logan, Utah) (Kirkham, 1985). Between 1000 and 1100 HR, two young, fully emerged leaf (first collared leaf) blades from each experimental unit were excised at the collar and immediately sealed inside a small, watertight, stainless-steel psychrometer chamber. The leaf was equilibrated at 25 °C for 5.5 h in a water bath before measuring water potential using the dewpoint method. Cooling time was 30 s. To measure ψ_s, two to ten young and fully emerged leaf blades were excised at the collar, placed in a microcentrifuge tube, and frozen in dry ice for 24 h (Thomas, 1987). After leaves thawed for 30 min, sap was expressed using a laboratory press (Fred S. Carver Inc., Wabash, Ind.). A 10-µL aliquot of the expressed sap was injected onto a filter paper disc that was placed in the sampling chamber of an osmometer (model 5500; Wescor) to measure ψ_s. Leaf pressure potential was calculated by subtracting ψ_s from ψ_L.

To determine SWC by TDR, holes to accommodate TDR probes were drilled in the side of PVC containers 10 cm below the soil surface. Two 17-cm-long stainless-steel probes were inserted horizontally. Clear silicone glue was used to seal the holes and anchor the probes.

In the second experiment, leaf osmotic potential at full turgor (ψ_s^{100}) was determined between 1000 and 1200 HR on the first day of the soil-drying cycle and on the day when SWC in individual containers declined to 12%. To assess ψ_s^{100}, 10 leaves from each experimental unit were excised, brought to full hydration by submerging in distilled water for 8 h at room temperature, blotted dry, and frozen at −15 °C for 24 h in a microcentrifuge tube. After leaves thawed, ψ_s^{100} was measured as described for ψ_s measurement. Leaf OA during this period was calculated as OA = $\psi_s^{100(b)}$ − $\psi_s^{100(a)}$, where $\psi_s^{100(b)}$ and $\psi_s^{100(a)}$ are the ψ_s^{100} before and after drought, respectively (Chapman and Auge, 1994).

When SWC in individual containers reached ≈8%, turf in each container was rewatered. Percent green coverage was rated visually 2 weeks after rewatering.

Containers were arranged in a completely randomized design with four replications. To minimize effects of greenhouse environmental variability, pots were rerandomized on each measurement day. Due to the effect of climatic conditions, dry-down duration was longer in the first study than in the second. Therefore, changes in SWC and ET rate over time during the two studies are presented separately. However, relationships between SWC and ψ_L or ψ_S were not statistically different between the first and second studies; therefore, data for parameter relationships were combined over studies for analyses. To simplify graphic presentation, SWC data were rounded to
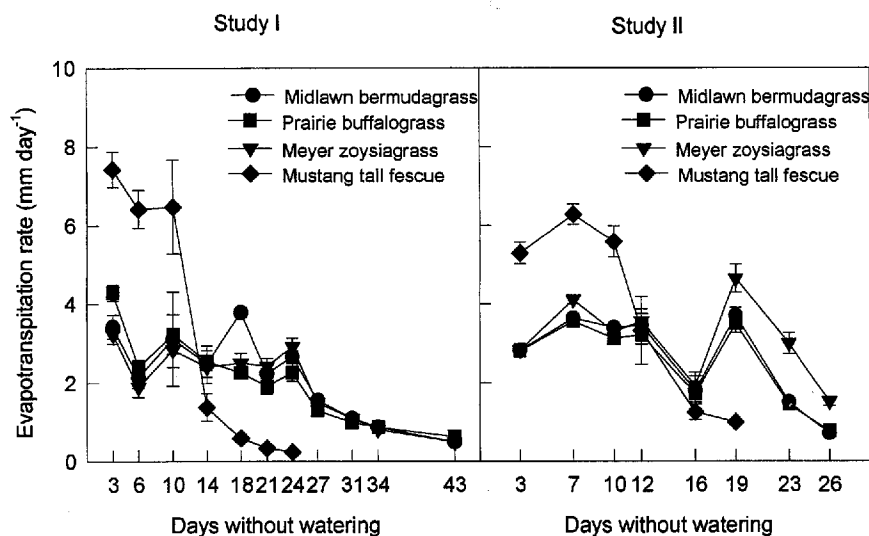
Study I / Study II

Fig. 2. Evapotranspiration (ET) of four turfgrasses after watering ceased. Each point represents the mean of four replications. Bars indicate SE.

130

1 of 16 preselected values, ranging from 12% to 36%, and ψ_L and ψ_S were plotted against SWC. Each mean represented the average of at least two observations, and the standard error for each was calculated. Data on shoot extension rate, leaf water content, green coverage, $\psi_S^{100(b)}$, $\psi_S^{100(a)}$, and OA were subjected to the analysis of variance, and means were separated using a protected LSD at $P <$ 0.05 (SAS, Cary, N.C.). Nonlinear least-squares regression was used to determine the relationship between ψ_p and ψ_L for each species.

Results and Discussion

EVAPOTRANSPIRATION AND TURF RESPONSE TO DROUGHT. Volumetric soil water content under each grass declined with time, and the initial rate of decline was greater for tall fescue than for warm-season turfgrasses (Fig. 1). In both studies, SWC under tall fescue fell to <15% within 10 to 12 d, whereas 18 to 28 d were required for soil under warm-season grasses to decline to a similar range. No significant differences occurred in SWC decline among warm-season grasses.

Rate of decline in SWC was associated with ET rate. Tall fescue exhibited a 70% to 130% higher ET rate than warm-season grasses during the first 10 d of dry down, during which SWC was >15% (Fig. 2). In an earlier field study, we reported that ET of 'Mustang' tall fescue was 19% to 35% higher than ET of the same three warm-season grasses (Qian et al., 1996b). However, tall fescue ET was significantly lower than ET of warm-season grasses after 12 to 15 d without watering, a response to limited soil water availability (Fig. 2). At this point, tall fescue exhibited significant leaf rolling. After 20 to 25 d without water, tall fescue appeared brown and dormant. Warm-season grasses exhibited drought symptoms after 25 d without water and appeared dormant after ≈40 to 45 d.

Tall fescue and zoysiagrass exhibited leaf rolling at ≈18%

SWC. This may be a drought avoidance strategy to reduce the transpiration surface area and enclose stomata in chambers with higher humidity (Turner and Jones, 1980). Buffalograss leaves exhibited an increasingly grayish appearance as SWC decreased. When SWC declined to ≈16%, buffalograss firing was evident on leaf tips. As SWC decreased further, lower buffalograss leaves appeared bleached. Buffalograss may employ this leaf firing strategy to reduce surface area for ET (Turner and Jones, 1980). Bermudagrass exhibited drought symptoms similar to those of buffalograss and zoysiagrass. Leaf blade tips rolled when SWC reached ≈16%. When SWC decreased further, lower leaves became bleached. Our results suggest that these grasses use different strategies to limit plant water loss and offset the deleterious effects of drought.

WATER RELATIONS CHARACTERISTICS. Leaf water content of tall fescue before dry down was 78%, which was higher ($P < 0.05$) than contents of bermudagrass (73%), buffalograss (68%), and zoysiagrass (67%). Bermudagrass leaf water content was higher ($P < 0.05$) than for buffalograss and zoysiagrass.

Under well-watered conditions, tall fescue had a mean ψ_L of −0.53 MPa, 0.41 MPa higher than the mean ψ_L of all warm-season turfgrasses (Fig. 3). However, tall fescue ψ_S (−1.57 MPa) was lower than that of warm-season grasses (Fig. 3). Therefore, tall fescue maintained a mean ψ_p of 1.04 MPa, 0.64 to 0.71 MPa higher than the ψ_p of all warm-season grasses. Tall fescue's higher ψ_p may have contributed to a leaf extension rate that was 42% to 77% higher than that of warm-season grasses under well-watered conditions (data not shown).

Among warm-season grasses, mean ψ_L under well-watered conditions decreased in the order of buffalograss (−0.81 MPa) > bermudagrass (−0.99 MPa) = zoysiagrass (−1.03 MPa). Ranking of grasses for mean ψ_S under well-watered conditions was similar to that for ψ_L with buffalograss (−1.16 MPa) > bermudagrass (−1.35 MPa) > zoysiagrass (−1.43 MPa). No significant differences in ψ_p were observed (0.31 to 0.40 MPa) among warm-season grasses.

Tall fescue ψ_L remained constant until SWC declined to ≈20% (Fig. 3). Buffalograss ψ_L remained unaffected until ≈18% SWC. Below these SWCs, ψ_L of tall fescue and buffalograss decreased rapidly. Leaf water potentials of bermudagrass and zoysiagrass declined slowly when SWC decreased from field capacity to 14% and 16% SWC, respectively. Below these points, ψ_L declined rapidly in bermudagrass and zoysiagrass.

Tall fescue maintained consistent ψ_S until SWC was ≈18% to 20%, and then ψ_S dropped rapidly (Fig. 3). Warm-season grasses exhibited slow declines in ψ_S until ≈16% SWC, when ψ_S dropped sharply. Leaf osmotic potential was less variable than ψ_L, possibly because it was less responsive to transient changes in the environment.

The decline in ψ_p with each unit of decline in ψ_L was greater for tall fescue and zoysiagrass than for buffalograss and bermudagrass (Fig. 4). This may explain partially why tall fescue and zoysiagrass leaves rolled relatively early in the stress period.
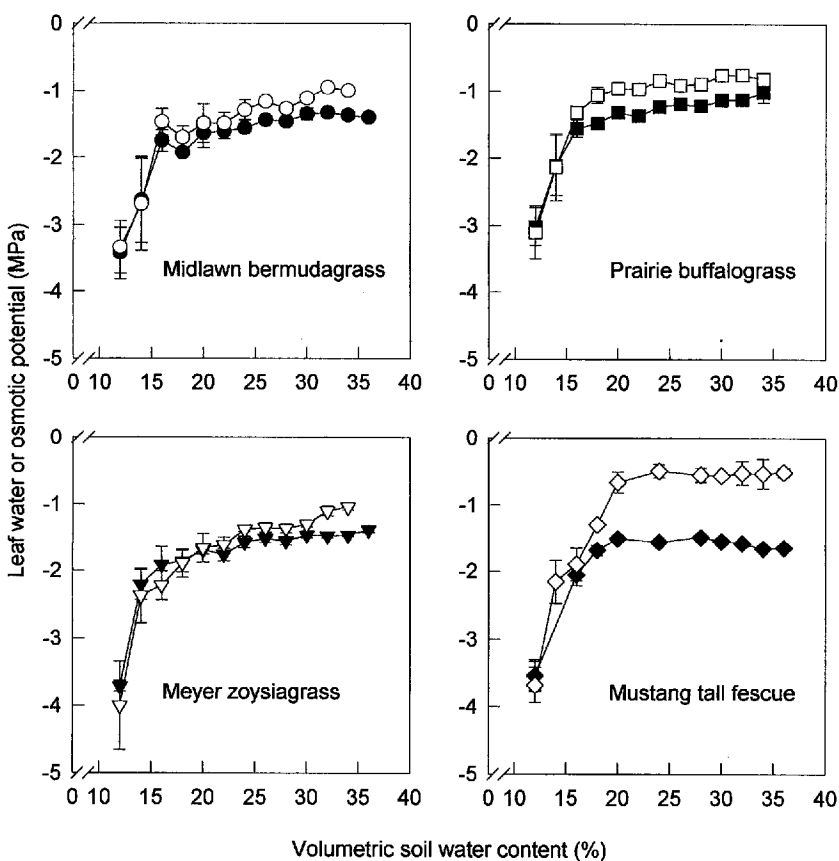

Fig. 3. Decline in leaf water potential and leaf osmotic potential of four turfgrasses with declining volumetric soil water content. Open symbols, leaf water potential; solid symbols, leaf osmotic potential. Bars represent SE of the mean. Each point is a mean of two to eight observations.
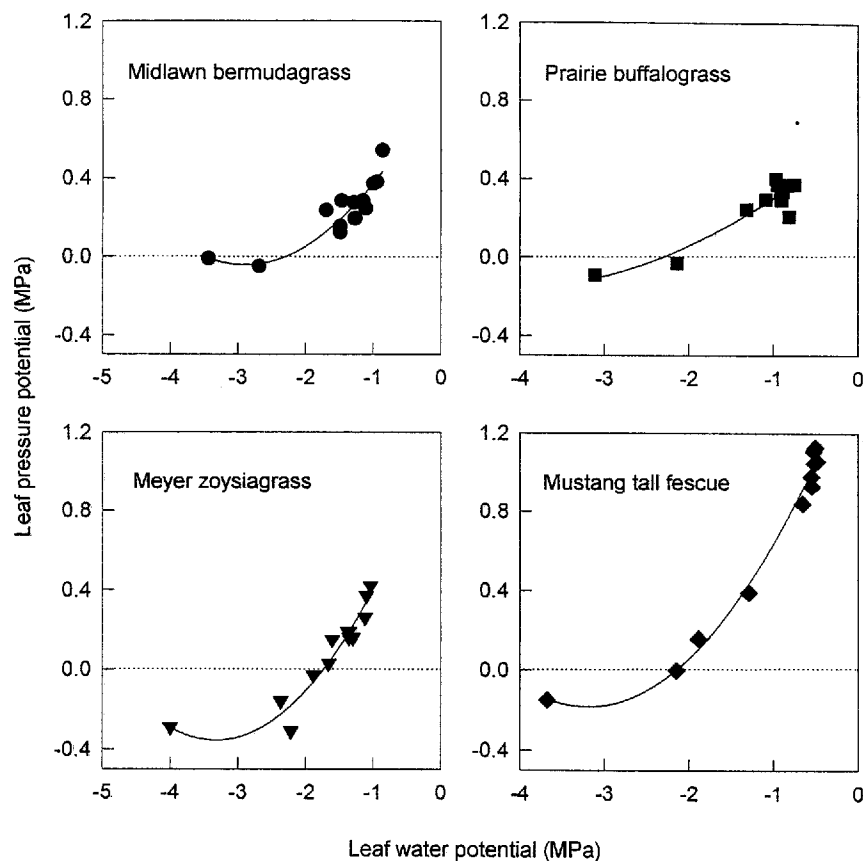
Fig. 4. Relationships between leaf pressure potential and leaf water potential of 'Midlawn' bermudagrass (y = 0.93 + 0.67x + 0.12x^2, R^2 = 0.84), 'Prairie' buffalograss (y = 0.62 + 0.37x + 0.04x^2, R^2 = 0.86), 'Meyer' zoysiagrass (y = 1.19 + 0.93x + 0.14x^2, R^2 = 0.93), and 'Mustang' tall fescue (y = 1.56 + 1.09x + 0.17x^2, R^2 = 0.98). Each point is a mean of two to eight observations.

grasses may have been a consequence of the rapid development of drought stress in containers where rooting was restricted. However, no significant OA was detected in the field during a 3-week drought period in Summer 1994 during which wilting was observed (data not presented). Similar values for OA in tall fescue were reported during a 21-d dry down in the greenhouse (White et al., 1992). Barker et al. (1993) evaluated OA of five warm- and cool-season forage grasses during drought. Osmotic adjustment of 0.48 to 0.68 MPa was noted in the cool-season grasses, reed canarygrass (*Phalaris arundinacea* L.), and smooth bromegrass (*Bromus inermis* Leyss.) (Barker et al., 1993). In the same study, OA of 0.76 to 1.25 MPa was observed in the warm-season grasses, indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), and big bluestem (*Andropogon gerardii* Vitman). Osmotic adjustment of 0.39 to 0.71 MPa was measured in four warm-season pasture grasses (Wilson et al., 1980).

RECOVERY FROM PROLONGED DROUGHT. All species were wilted severely and brown when SWC dried to ≈8%. Two weeks after rewatering, percent green coverage was highest for 'Prairie' buffalograss (50%), followed by 'Meyer' zoysiagrass (22%), and then 'Midlawn' bermudagrass (14%). 'Mustang' tall fescue exhibited the lowest green coverage (4%) 2 weeks after rewatering.

A positive correlation (r = 0.66) was observed between OA and green coverage 2 weeks after watering. Osmotic adjustment assists in turgor maintenance, which allows photosynthesis and leaf expansion to continue during periods of drought (Hsiao, 1973; Ludlow et al., 1985). Photosynthates produced during this period may aid in survival. Hsiao et al. (1984) suggested that OA is as important to plant survival as it is to turgor maintenance. Some evidence indicates that leaf OA in graminoids contributes more to prolonging shoot survival during drought than to maintaining leaf elongation (Toft et al., 1987; Wilson and Ludlow, 1983).

Based on responses to drought, drought survival, and the magnitude of OA, warm-season grasses were superior to tall fescue in tolerance of low internal ψ_L. Our results support the views of Ludlow (1989) and Sinclair and Ludlow (1986), who suggested that drought avoiders maintain higher ψ_L, have low dehydration tolerance, and generally display little OA.

These experiments have provided information that defines drought resistance mechanisms in selected turfgrasses. 'Mustang' tall fescue relied primarily on a deep, extensive root system to maximize water uptake (Qian et al., 1996a). Osmotic adjustment

Although all species exhibited zero ψ_P at a ψ_L of 1.8 to 2.3 MPa, ψ_P for wilting symptoms (sign of leaf rolling or leaf firing) was much higher for tall fescue (≈0.35 MPa) than for all warm-season turfgrasses (≈0 MPa). Negative ψ_P were observed for warm-season grasses. This may have been because 1) the membrane-rupture technique used to measure ψ_S in this study can overestimate ψ_S at low ψ_L (Tyree, 1976); 2) leaf matric potential can become significant during severe drought stress (Hsiao, 1973) and this was ignored; or 3) water potential and osmotic potential were not determined on the same leaves.

Osmotic adjustment was greatest in buffalograss (0.81 MPa) and zoysiagrass (0.77 MPa), and lowest in tall fescue (0.34 MPa) (Table 1). Bermudagrass exhibited an intermediate OA (0.60 MPa). The minimal OA of tall fescue relative to warm-season

Table 1. Leaf osmotic potential at full turgor before ($\psi_S^{100(b)}$) and after ($\psi_S^{100(a)}$) drought stress and magnitude of osmotic adjustment (OA) and comparative OA of four container-grown turfgrasses in the greenhouse.[z]

Grass	$\psi_S^{100(b)}$(MPa)	$\psi_S^{100(a)}$(MPa)	Magnitude of OA (MPa)	Comparative OA(%)[x]
'Midlawn' bermudagrass	1.12 bc[y]	1.71 b	0.60 b	54
'Prairie' buffalograss	1.08 c	1.89 a	0.81 a	78
'Meyer' zoysiagrass	1.15 b	1.92 a	0.77 a	67
'Mustang' tall fescue	1.31 a	1.65 b	0.34 c	26

[z]Numbers represent the mean of four replications.

[y]Means in the same column followed by the same letter are not different at P < 0.05 by Fisher's protected LSD.

[x]Comparative OA (%) = (magnitude of OA/$\psi_S^{100(b)}$) × 100.

in tall fescue was low, and recovery was poor after exposure to severe drought. 'Prairie' buffalograss developed a relatively deep root system, had a low shoot to root ratio, and low ET rate (Qian et al., 1996a, 1996b). 'Prairie' buffalograss also maximized OA when subjected to declining SWC. 'Midlawn' bermudagrass exhibited rooting and ET similar to 'Prairie' buffalograss (Qian et al., 1996a, 1996b). However, OA and survival rate after severe drought for 'Midlawn' bermudagrass were inferior to 'Prairie' buffalograss and better than 'Mustang' tall fescue. 'Meyer' zoysiagrass had a relatively shallow root system and intermediate ET rate (Qian et al., 1996a, 1996b). However, 'Meyer' exhibited a high level of OA that may have aided recovery after drought stress.

Literature Cited

Aronson, L.J., A.J. Gold, and R.J. Hull. 1987. Cool-season turfgrass response to drought stress. Crop Sci. 27:1261–1266.

Barker, D.J., C.Y. Sullivan, and L.E. Moser. 1993. Water deficit effects on osmotic potential, cell wall elasticity, and proline in five forage grasses. Agron. J. 85:270–275.

Chapman, D.S. and R.M. Auge. 1994. Physiological mechanisms of drought resistance in four native ornamental perennials. J. Amer. Soc. Hort. Sci. 119:299–306.

Fry, J.D. and J.D. Butler. 1989. Responses of tall fescue and hard fescue to deficit irrigation. Crop Sci. 29:1536–1541.

Gibeault, V.A., J.L. Meyer, V.B. Youngner, and S.T. Cockerham. 1985. Irrigation of turfgrass below replacement of evapotranspiration as a means of water conservation: performance of commonly used turfgrasses, p. 347–356. In: F. Lemaire (ed.). Proc. 5th Intl. Turfgrass Res. Conf., Avignon, France.

Hsiao, T.C. 1973. Plant responses to water stress. In: W.R. Briggs, P.C. Green, and R.L. Jones (eds.). Annu. Rev. Plant Physiol. 24:519–570.

Hsiao, T.C., J.C. O'Toole, E.B. Yambao, and N.C. Turner. 1984. Influence of osmotic adjustment on leaf rolling and tissue death in rice. Plant Physiol. 75:338–341.

Kirkham, M.B. 1985. Techniques for water-use measurements of crop plants. HortScience 20:993–1001.

Levitt, J. 1980. Response of plants to environmental stresses. Water, radiation, salt, and other stresses. vol. 2. Academic Press, New York.

Ludlow, M.M. 1989. Strategies in response to water stress, p. 269–281. In: H.K. Kreeb, H. Richter, and T.M. Hinkley (eds.). Structural and functional response to environmental stress: Water shortage. SPB Academic Press, The Netherlands.

Ludlow, M.M., M.J. Fisher, and J.R. Wilson. 1985. Stomatal adjustment to water deficits in three tropical grasses and a tropical legume grown in controlled conditions and in the field. Austral. J. Plant Physiol. 12:131–149.

Morgan, J.M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. Austral. J. Agr. Res. 34:607–614.

Qian, Y.L., J.D. Fry, and W.S. Upham. 1996a. Rooting and drought avoidance of four turfgrasses in Kansas. (In press.)

Qian, Y.L., J.D. Fry, S.C. Wiest, and W.S. Upham. 1996b. Estimation of turfgrass evapotranspiration using atmometers and the Penman-Monteith model. Crop Sci. 36:699–704.

Sinclair, T.R. and M.M. Ludlow. 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Austral. J. Plant Physiol. 13:329–341.

Thomas, H. 1987. Physiological responses of drought of Lolium perenne L.: Measurement of, and genetic variation in, water potential, solute potential, elasticity and cell hydration. J. Expt. Bot. 38:115–125.

Toft, N.L., S.J. McNaughton, and N.J. Georgeadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an east African grass, Eustachys paspaloides. Austral. J. Plant Physiol. 14:211–226.

Turner, N.C. and M.M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation, p. 87–103. In: N.C. Turner and P.J. Kramer (ed.). Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Tyree, M.T. 1976. Negative turgor pressure in plants: Fact or fallacy? Can. J. Bot. 54:2738–2746.

White, R.H., M.C. Engelke, S.J. Morton, and B.A. Ruemmele. 1992. Competitive turgor maintenance in tall fescue. Crop Sci. 32:251–256.

Wilson, J.R. and M.M. Ludlow. 1983. Time trends for change in osmotic adjustment and water relations of leaves of Cenchrus ciliaris during and after water stress. Austral. J. Plant Physiol. 10:15–24.

Wilson, J.R., M.M. Ludlow, M.J. Fisher, and E.D. Schulze. 1980. Adaptation to water stress of leaf water relations of four tropical forage species. Austral. J. Plant Physiol. 7:207–220.

Wright, G.C., R.C.G. Smith, and J.M. Morgan. 1983. Differences between two grain sorghum genotypes in adaptation to drought stress. III. Physiological responses. Austral. J. Agr. Res. 34:637–651.

Youngner, V.B. 1985. Physiology of water use and water stress, p. 37–43. In: V.A. Gibeault and S.T. Cockerham (ed.). Turfgrass water conservation. Univ. of Calif., Riverside, Coop. Ext. Publ. 21405.

J. Amer. Soc. Hort. Sci. 122(1):129–133. 1997.

133