Relationships between Water Use Efficiency, Carbon Isotope Discrimination, and Turf Performance in Genotypes of Kentucky Bluegrass during Drought

J. S. Ebdon* and K. L. Kopp

ABSTRACT

Carbon-13 discrimination (Δ) and water use efficiency (WUE) have been largely ignored in turfgrass. Turfgrass performance under drought may be improved by selecting for low Δ, which has been shown to be negatively correlated with WUE. The objectives of this 2-yr greenhouse study were (i) to compare Δ and WUE in 12 genotypes of Kentucky bluegrass (*Poa pratensis* L.) with evapotranspiration (ET) and rooting for assessing turf performance under drought, and (ii) to determine the relative importance of ET in drought resistance by comparing diverse ET genotypes (6 low and 6 high) during drydown. Clipping dry weight to ET ratio (WUE) was evaluated with sand-filled weighing lysimeters (20-cm diam. by 65-cm depth) during two 4-d periods (Days 1 to 4 and 5 to 8) in 2002 and 2003. Carbon (^{13}C/^{12}C) analysis of leaf clippings was used to derive Δ values. Time domain reflectometry (TDR) was used to measure changes in volumetric soil moisture content (VSMC) at the 8.25-, 17.5-, 35.0-, and 52.5-cm depths to indicate moisture uptake and rooting activity. Drought resistance was visually assessed as wilt and leaf-firing symptoms. Low- and high-ET genotypes were similar in wilt and leaf firing, suggesting low ET may not be relevant in drought survival. Deep rooting at the 52.5-cm depth and higher ET as soils dried were associated with less leaf firing. The WUE at Days 5 to 8 was comparable in some years with rooting. The Δ was not always reliable in assessing WUE, but turf performance under drought was correlated with Δ. Low Δ values were associated with less wilt ($r = 0.59, P \leq 0.05$) and leaf firing ($r = 0.58, P \leq 0.05$), suggesting that Δ may be a useful selection criterion for superior performance under limiting soil moisture.

Under moisture-limiting environments, productivity in crop plants may be increased by improving WUE (biomass to water loss ratio) (Ehleringer et al., 1993). In turfgrass, WUE may not be relevant because the rate of leaf growth under nonlimiting soil moisture has been shown to be poorly correlated with turf quality (Mehall et al., 1984). Accordingly, superior yield may not necessarily equate to superior turfgrass performance (Shearman, 1985; Youngner, 1985). Drought stress affects visual turf quality, growth rate, ET, and recuperative potential (Beard, 1973). Under limited moisture, the ability to maintain quality turf is dependent on leaf growth (Aronson et al., 1987). Therefore, superior yield (productivity), and in turn, WUE may be an important component of turfgrass performance in moisture-limiting environments.

As the demand for water and higher quality turf continues to increase, efficient and effective methods for assessing germplasm adapted to minimal water resources will be needed. Several physiological methods have been suggested for drought resistance screening in turfgrass, including leaf water potential (Huang et al., 1998; Perdomo et al., 1996), relative water content (Aronson et al., 1987; Huang and Gao, 1999; Zhoa et al., 1994), photosynthetic capacity and leaf conductance (Bonos and Murphy, 1999; Huang and Gao, 1999; Perdomo et al., 1996), leaf canopy temperature (Bonos and Murphy, 1999; Perdomo et al., 1996; Zhoa et al., 1994), and electrolyte leakage (Marcum, 1998; Zhoa et al., 1994). Hanson and Nelson (1980) suggested that effective screening techniques in breeding for drought resistance should be (i) highly correlated with drought resistance, (ii) rapid with high resolution requiring small plant samples, and (iii) nondestructive. To that end, stable carbon isotope composition (δ) may be a potentially valuable method for evaluating turfgrass for drought resistance.

Carbon isotope analysis integrates the ratio of stable isotopes of carbon (^{13}C/^{12}C, R) across the life of the particular plant tissue being analyzed. Plants that fix carbon by the C_3 pathway are depleted in the heavier isotope when compared with the isotopic ratio of air (Farquhar and Richards, 1984). This fractionation between ^{13}C and ^{12}C is caused by differences in the diffusivities in air between the heavier and lighter isotopes and by the initial carboxylating enzyme (rubisco), which discriminates against the heavier isotope. The resulting biological discrimination against carbon-13 by C_3 plants (Δ, derived from δ measurements) has been shown to be negatively correlated with WUE in a wide range of plants, including cool-season grasses (Ebdon et al., 1998a; Johnson and Basset, 1991; Johnson and Yangyang, 1999). Investigations into the relationship between Δ and WUE in turfgrass have been limited to well-watered conditions (Ebdon et al., 1998a), which may not be relevant to drought (Farquhar and Richards, 1984).

The inverse relationship underlying Δ and WUE is stomatal conductance (Farquhar et al., 1989). As water becomes plant limiting, some degree of stomatal closure occurs. Discrimination against ^{13}C decreases as water stress increases because the ^{13}C/^{12}C ratio increases in stressed C_3 leaves, and rubisco has less opportunity to discriminate. Studies have shown that Δ is a heritable trait and WUE can be increased by selecting for low Δ (Johnson and Yangyang, 1999; Johnson et al., 1990; Martin et al., 1999). Although WUE can be accurately measured with instantaneous gas exchange measurements, these measurements do not provide information across an extended period of time. Carbon is continually

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J.S. Ebdon, Dep. of Plant and Soil Sci., 12F Stockbridge Hall, Univ. of Massachusetts, Amherst, MA 01003; K.L. Kopp, Dep. of Plants, Soils, and Biometeorology, Utah State Univ., Logan, UT 84322. Received 14 Sept. 2003. *Corresponding author (sebdon@pssci.umass.edu).

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677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: Δ, carbon-13 discrimination; δ, stable carbon isotope composition; ET, evapotranspiration; TDR, time domain reflectometry; VSMC, volumetric soil moisture content; WUE, water use efficiency.

fixed by the leaf, thus Δ provides an integrated average across the life of the tissue. This suggests that Δ may better differentiate among genotypes than instantaneous gas exchange measurements.

Superior drought resistance includes avoidance (low ET and deep rooting) and tolerance mechanisms (Beard, 1989). Turfgrass with low ET (determined under nonlimiting soil moisture) has been suggested as a desirable trait for turfgrasses growing under limited water (Beard, 1989; Salaiz et al., 1991). Others have suggested that the low ET model may not be appropriate for selecting turfgrass for prolong periods of moisture stress (Keeley and Koski, 1995; Perdomo et al., 1996). Additionally, water use measurements under nonlimiting soil moisture are not necessarily good predictors of water use under stress (Fernandez and Love, 1993). The suitability of the low ET model for selecting turfgrass for moisture stress environments needs further evaluation.

Our objectives were (i) to compare drought resistance in diverse-water-use genotypes, and (ii) to determine if Δ and WUE are important factors for assessing Kentucky bluegrass performance during drought in comparison with ET and rooting.

MATERIALS AND METHODS

Cultivar Selection and Establishment

Authentic seed of 12 Kentucky bluegrass genotypes were obtained from breeders for study. The 12 selections included six low-water-use genotypes ('Freedom', 'Indigo', 'Midnight', 'Nassau', 'Ram I', and 'Suffolk') and six high-water-use genotypes ('Abbey', 'Eclipse', 'Ginger', 'Kenblue', 'Livingston', and 'South Dakota Certified'). The low- and high-water use types represent a diverse range (top and bottom 5%) in ET based on previous studies involving 61 Kentucky bluegrass genotypes (Ebdon et al., 1998b).

In July 2001, genotypes were seeded at 0.3 g of pure live seed to 20-cm-diam. by 65-cm-deep lysimeters. Each genotype was replicated four times. Lysimeters were filled with a prepared rootzone (4–1–1 sand–soil–peat, v/v) with the final mixture containing 89.8 ± 0.2% sand, 7.8 ± 0.2% silt, and 2.4 ± 0.2% clay. Peat humus was used as the amending organic matter source and the final rootzone mixture had an organic matter content (loss on ignition) of 2.5 ± 0.2%. Approximately 70.2 ± 1.6% of the sand fraction was in the coarse and medium class size range. The surface of the rootzone was approximately 1.25 cm below the top of the lysimeter. Before establishment, each lysimeter was amended according to soil test with 103 g dolomitic lime, 8.2 g potassium sulfate (0–0–41.5), 10.3 g superphosphate (0–8.8–0), 2.2 g urea (45–0–0), and 7.4 g of 28–2.2–10 (N–P–K). During the establishment phase (about 30 d), containers were kept in a mist house and then moved to a semicontrolled greenhouse environment. After the establishment phase ended, grasses were mowed twice weekly at 5 cm, fertilized weekly with half-strength Hoagland's solution, and were watered to prevent visual moisture stress.

Rooting Potential

The small turf area within individual lysimeters did not permit soil cores to be removed to assess rooting potential, so changes in VSMC were measured at four depths (8.25, 17.5, 35, and 52.5 cm) as an alternative for assessing rooting potential (Jiang and Marcum, 1994; Qian and Fry, 1996; Qian et al., 1997; Sheffer et al., 1987). The VSMC was measured with TDR (Mesa Systems, Medfield, MA). In mid-February of 2002, three TDR rods measuring 17.5 cm in length and spaced 3.5 cm apart were inserted horizontally into predrilled holes along the lysimeter wall of each container. The center rod of each three-rod set was positioned at the four previously mentioned depths. Rods were sealed to the outside wall of the lysimeter with silicone glue. The same grass-covered lysimeters were used throughout the study (2002 and 2003).

Water Use Efficiency and Isotopic Analysis

Evapotranspiration rates were measured with the gravimetric water balance method as described by Ebdon et al. (1998a). A 4-d cycle was used in calculating ET. At the start of a drydown cycle, containers were weighed and watered to a predetermined standard container capacity approximating field capacity. The VSMC at container capacity was measured by TDR at the start of each drydown in 2002 and 2003. In 2002, VSMC at 8.25-, 17.5-, 35-, and 52.5-cm depths were 11.6 ± 2.1, 10.3 ± 1.9, 14.9 ± 1.2, and 27.1 ± 2.1 $m^3\ m^{-3}$, respectively. In 2003, VSMC at container capacity for 8.25-, 17.5-, 35-, and 52.5-cm depths were 10.2 ± 1.3, 9.9 ± 1.3, 15.9 ± 1.4, and 31.1 ± 2.4 $m^3\ m^{-3}$, respectively. Turfgrass water loss during a 4-d period was used as the transpirational component in calculating WUE for that 4-d period. Leaf biomass accumulated above a 5-cm mowing height was used as the productivity component. Leaf clippings were harvested and immediately oven dried at 70°C for 48 h. The WUE was calculated as dry weight to water loss ratio (mg mL^{-1}).

Dried leaf tissues were ground to a powder to homogenize the tissues for carbon analysis according to the methods of Ehleringer (1991). A well-mixed 10-mg subsample was sent to the Stable Isotope Facility Ratio for Environmental Research at the University of Utah for isotopic analysis; see Smedley et al. (1991) for details about the C analysis used in this study. The carbon isotope composition ($\delta^{13}C$) of a sample was determined as

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000, \qquad [1]$$

expressed in units of per thousand (‰). The δ of a sample according to Eq. [1] was determined by comparing ^{13}C to ^{12}C ratio (R) of a sample to the Peedee belemite carbonate formation standard. Discrimination (Δ) of a sample was calculated as

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_p), \qquad [2]$$

where δ_a is the C isotopic composition of the source air and δ_p is the C isotopic composition of the plant sample. In calculating Δ values of a sample, we assumed the δ_a (greenhouse air) to be −8‰ (Johnson et al., 1990), the isotopic value of air measured under well-mixed conditions. The δ_a in a greenhouse environment is likely to be enriched in the heavier isotope (more negative than −8‰, probably −10 to −13‰). The −8‰ assumption is less important in this study because our objective is the relationship between Δ and WUE, so we do not view Δ in absolute terms as a direct measure of WUE.

Drought Resistance Assessment

To assess turfgrass drought resistance, Kentucky bluegrass genotypes were exposed to a drydown (water withheld) in 2002 and 2003. At the beginning of each drydown period, grasses were at 100% green cover. Before the start of each drydown evaluation, lysimeter columns were irrigated to container capacity and then initial TDR-VSMC measurements were made at all depths. The 2002 drydown evaluation period began 24 June (Replicate 1) and ended on 9 July (Replicate 4) while the 2003 drought evaluation began 20 June (Replicate 1) and ended on 8 July (Replicate 4).

Measurements taken during the drydown, including ET, clipping yields, and TDR-VSMC, were taken on all genotypes within a replicate (by block) on a given day. Therefore, four consecutive days were required to complete measurements on all four replicates. Results are reported here as sequential 4-d drydown periods. Termination of a drydown occurred only after sufficient drought injury (loss in green color) was observed to assess drought resistance. Three sequential 4-d periods were completed in 2002 (Days 1 to 4, 5 to 8, and 9 to 12) and four sequential 4-d cycles were completed during 2003 (Days 1 to 4, 5 to 8, 9 to 12, and 13 to 16). The cooler temperatures experienced in 2003 required an extra 4-d drydown cycle to achieve sufficient tissue dehydration to effectively evaluate drought resistance. Greenhouse temperatures were monitored hourly with an air-gas thermocouple (model 422314, Extech Instruments, Vernon Hills, IL). Mean daily temperatures during the 2002 drydown were 30.3 ± 1.6°C (Days 1 to 4), 32.1 ± 2.6°C (Days 5 to 8), and 31.1 ± 3.1°C (Days 9 to 12), and in 2003 daily temperatures averaged 27.1 ± 5.9°C (Days 1 to 4), 30.9 ± 2.2°C (Days 5 to 8), 30.6 ± 1.8°C (Days 9 to 12), and 32.3 ± 1.9°C (Days 13 to 16). No supplemental lighting was used during drydown in 2002 and 2003.

The WUE measurements were terminated whenever drought stress was severe enough to cause insufficient leaf growth for analysis. Leaf growth, and in turn, WUE ceased by Day 8 (end of the 2nd 4-d drydown cycle) in 2002 and 2003. Similarly, VSMC with TDR technology was discontinued whenever soil moisture depletion at a particular TDR depth was statically equivalent to 0 m^3 m^{-3} VSMC. Specifically, after Day 4 of the drydown in 2002 and 2003, the average VSMC at the 8.25-cm depth was 0.4 ± 0.5 m^3 m^{-3} and 0.6 ± 0.8 m^3 m^{-3} VSMC, respectively. Therefore, TDR-VSMC measurements at the 8.25-cm depth were terminated after Day 4 (end of the 1st 4-d drydown cycle). Additionally, after Day 12 in 2003 (end of the third 4-d drydown cycle), TDR-VSMC measurements at the 17.5-cm depth averaged 1.1 ± 0.8 m^3 m^{-3} VSMC and therefore measurements were terminated.

In 2002, wilt was assessed at Day 8 (end of the 2nd 4-d drydown cycle) and leaf firing was assessed at Day 12 (end of the 3rd 4-d drydown cycle). During the 2003 drydown, wilt was assessed at Day 12 (end of the 3rd 4-d drydown cycle) and leaf firing was assessed at Day 16 (end of the 4th 4-d drydown cycle). Wilting, which occurs before leaf firing, indicates that death of the tissues are imminent. Leaf firing occurs later in the drydown and is an indication of severe tissue dehydration. Wilting was a visual assessment of the percentage of leaves showing leaf fold, leaf roll, and blue-gray discoloration. Leaf firing symptoms were expressed as the percentage of leaves exhibiting yellowing, tan to brown discoloration. Wilt and leaf-firing symptoms are an integration of drought resistance (avoidance and tolerance) mechanisms; therefore, both mechanisms were active under the conditions imposed in these studies.

Statistical Analysis

The experimental design was a randomized complete block. Genotypes within a replicate were randomized (blocked) across the greenhouse bench. Measurements were taken on all genotypes within a given replicate on the same day. Measurements were repeated daily by replicate until all replicates had been assessed before terminating a drydown. Analysis of variance procedures were used to partition the total sum of squares (SS) according to preplanned treatment and experimental design structure. Genotype treatment SS were partitioned into single degrees of freedom, orthogonal contrasts to test for differences between low- vs. high-water-use genotypes, and to compare genotypes within low- and high-water use groups. Statistical significance at $\alpha = 0.10$ and smaller are reported in tables to summarize the relative importance of genotype main effects and orthogonal contrasts. Least significant difference values are reported for other comparisons at the 0.05 level. Year-to-year interactions were detected; therefore, data for each year are presented individually. Correlation coefficients (*r*) were computed to assess the predictive value of WUE, Δ, rooting (TDR-VSMC), and ET for turf performance (wilt, leaf firing) under moisture-limiting environments.

RESULTS AND DISCUSSION

Water Use Efficiency and Carbon Isotope Discrimination

If Δ and WUE are to be useful in selecting Kentucky bluegrass for improved drought resistance, then genotypes must differ in Δ and WUE and in turn correlate with turf performance under drought. According to genotype main effects or preplanned contrasts, genotypes in 2002 and 2003 differed significantly in WUE and Δ during the first and second 4-d periods (Days 1 to 4 and 5 to 8, Tables 1 and 2, respectively). The Δ values during the 2002 drydown ranged from 20.58 (Midnight) to 21.48‰ (Ginger) during Days 1 to 4 (Table 1). During Days 5 to 8, Δ values ranged from 20.32 (Midnight) to 21.18‰ (Kenblue) (Table 2). During the 2003 drydown, carbo-13 discrimination ranged from 21.16 (Midnight) to 21.89‰ (Ginger) during Days 1 to 4 (Table 1) and ranged from 20.83 (Ram I) to 21.57‰ (Abbey) during Days 5 to 8 (Table 2). These ranges in Δ reported here are consistent with those reported elsewhere for Kentucky bluegrass (Ebdon et al., 1998a). Year-to-year variation (2002 to 2003) in Δ values among genotypes were positively correlated at Days 1 to 4 ($r = 0.72$, $P \leq 0.01$) and 5 to 8 ($r = 0.87$, $P \leq 0.001$) indicating Δ values were relatively constant across years.

Ranking of genotypes based on Δ were positively correlated ($r = 0.87$, $P \leq 0.001$) across the two 4-d drydown periods during the 2002 and 2003 drydown. Wilting was assessed at the end of the second 4-d cycle in 2002 (Day 8, Table 2) and by the end of the third 4-d cycle in 2003 (Day 12, Table 3). Therefore, soil moisture was becoming growth limiting during these periods, indicating Δ was stable across diverse soil moisture environments (nonlimiting and moisture limiting). The Δ declined with soil moisture and Δ values were consistently lower in 2002 and 2003 for genotypes at Days 5 to 8 (Table 2) compared with Days 1 to 4 (Table 1). Our results are similar with other studies (Farquhar and Richards, 1984; Johnson et al., 1990), where conditions of low available soil moisture produced tissues of low Δ. In theory, these results suggest that decreasing soil moisture during drydown decreased leaf conductance and intercellular CO_2 levels, which in turn lowered Δ.

Kentucky bluegrass WUE in 2002 ranged from 0.25 (Ginger) to 0.48 mg mL^{-1} (Kenblue) at Days 1 to 4 (Table 1), and ranged from 0.07 (Freedom) to 0.16 mg mL^{-1} (Indigo) during Days 5 to 8 (Table 2). In 2003,

Table 1. Significance of variances and genotype means for evapotranspiration (ET), volumetric soil moisture content (VSMC) by soil depth, carbon-13 discrimination (Δ), and water use efficiency (WUE) at Days 1 to 4 during drydown (2002 and 2003).

	2002							2003						
		Change in VSMC by depth, cm							Change in VSMC by depth, cm					
	ET	8.25	17.5	35	52.5	Δ	WUE	ET	8.25	17.5	35	52.5	Δ	WUE
Source of variation							*P* values							
Blocks	***	*	†	***	†	***	***	***	**	*	***	***	ns‡	***
Genotype	*	*	ns	ns	ns	***	***	*	*	ns	ns	ns	**	*
Low vs. high§	**	*	ns	ns	ns	***	*	*	ns	ns	ns	ns	**	*
Among low¶	ns	ns	ns	ns	*	ns	*	†	ns	ns	ns	ns	†	ns
Among high¶	ns	*	ns	ns	ns	***	***	ns	†	ns	ns	ns	*	ns
							Genotype means							
Low water use	mm d^{-1}	m^3 m^{-3}				‰	mg mL^{-1}	mm d^{-1}	m^3 m^{-3}				‰	mg mL^{-1}
‘Freedom’	8.0	8.1	5.0	2.8	1.0	20.84	0.31	6.6	6.9	5.6	5.2	3.2	21.50	0.71
‘Indigo’	8.1	9.3	4.8	2.7	1.7	20.76	0.42	6.6	7.1	4.8	4.4	3.5	21.43	0.77
‘Midnight’	8.4	6.8	4.7	3.5	2.0	20.58	0.36	6.6	6.2	5.0	4.8	4.0	21.16	0.63
‘Nassau’	8.7	7.8	4.6	2.9	0.9	20.97	0.33	7.0	7.5	4.2	4.3	2.8	21.68	0.54
‘Ram I’	8.1	9.0	4.1	2.5	0.9	20.88	0.29	7.0	7.9	6.1	5.3	3.4	21.18	0.70
‘Suffolk’	8.0	8.7	5.6	3.2	0.9	20.87	0.30	6.4	8.0	5.3	4.6	2.9	21.52	0.62
Mean	8.2	8.3	4.8	2.9	1.2	20.82	0.34	6.7	7.2	5.1	4.8	3.3	21.41	0.66
High water use														
‘Abbey’	8.9	11.5	6.6	2.7	1.1	21.24	0.31	6.6	7.3	5.6	5.0	3.6	21.80	0.71
‘Eclipse’	8.4	8.8	4.5	3.0	1.5	20.69	0.35	6.9	7.3	5.0	5.1	3.8	21.38	0.62
‘Ginger’	8.4	10.4	6.0	3.3	1.3	21.48	0.25	6.8	8.8	6.3	5.2	3.6	21.89	0.46
‘Kenblue’	8.7	8.7	4.8	3.2	1.2	21.30	0.48	6.7	7.3	5.2	4.8	2.9	21.80	0.59
‘Livingston’	8.4	6.8	3.8	2.8	1.3	20.63	0.41	6.8	6.4	3.7	4.2	3.7	21.55	0.60
‘SD Certified’	8.8	10.6	5.8	2.9	1.4	21.16	0.44	7.2	7.4	5.6	5.1	4.2	21.32	0.48
Mean	8.6	9.5	5.3	3.0	1.3	21.08	0.38	6.8	7.4	5.2	4.9	3.0	21.62	0.58
LSD (0.05)	0.6	2.9	ns	ns	0.9	0.30	0.09	0.4	1.4	ns	ns	ns	0.38	0.18
CV, %	4.6	22.4	34.4	22.6	47.7	1.0	17.0	4.6	13.3	25.6	12.8	27.0	1.2	20.3

* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.
† Significant at the 0.1 level.
‡ ns = not significant.
§ Single df test for the difference between the combined means for low- vs. high-water-use genotypes.
¶ Test for the differences within low- or high-water-use genotypes.

WUE ranged from 0.46 (Ginger) to 0.77 mg mL^{-1} (Indigo) at Days 1 to 4 (Table 1), and ranged from 0.05 (Kenblue) to 0.16 mg mL^{-1} (Indigo) during Days 5 to 8 (Table 2). Ranking of genotype WUE across the two 4-d periods of diverse soil moisture were positively correlated ($r = 0.66$, $P \leq 0.05$) in 2002 but not in 2003 ($r = 0.41$, $P > 0.10$). Genotypic variation in WUE was not as stable under variable levels of soil moisture as Δ values.

The WUE under limiting soil moisture (Days 5 to 8) was lower compared with well-watered conditions (Days 1 to 4) by 0.25 mg mL^{-1} (2002 drydown) and 0.50 mg mL^{-1} (2003 drydown). Averaged across years, clipping production accumulated above a 5-cm base mowing height during Days 5 to 8 of the drydown decreased by 75% of well-watered conditions (Days 1 to 4), while ET rates at Days 5 to 8 were only 15% lower. This disproportionately greater decline in leaf growth rate relative to ET (and in WUE) under moisture stress has been reported in other studies (Aronson et al., 1987). These results generally contradict crop (yield) studies in which WUE increases with water deficits (Craufurd et al., 1999; Johnson et al., 1990), although a decrease in WUE with water stress has been observed (Heitholt, 1989). In yield studies, however, WUE is generally based on whole-plant productivity and not leaf clippings collected above a base mowing height.

There are limitations to the use of clipping dry matter accumulation as an indicator of dry matter accretion. First, carbon allocated to roots, tillers, and rhizomes are not included in the clipping dry matter measurement. Kentucky bluegrass genotypes tolerant to stress (heat and drought) may exhibit greater root weights (Bonos and Murphy, 1999), higher net photosynthetic rates (Jiang and Huang, 2000), and greater carbon allocated to roots and carbohydrate reserves (Watschke et al., 1970). Second, dry matter accumulations above a base mowing height can be affected by genotypic differences in growth habit (Ebdon et al., 1998a). Common-type genotypes used in this study such as Kenblue and South Dakota Certified that have an erect leaf orientation and rapid vertical leaf extension rates may allocate more photosynthate to leaf growth during periods of favorable soil moisture than slower-growing, compact types such as Indigo and Midnight. These factors may affect the relationship between WUE and Δ.

During Days 1 to 4 of the 2002 and 2003 drydown, WUE and Δ were not correlated (Fig. 1 and 2). Common-type genotypes (Kenblue and South Dakota Certified) had higher-than-expected WUE (clipping dry weight to water loss ratio) in relationship to their corresponding Δ values during 2002 (Fig. 1). Theory predicts that WUE for Kenblue and South Dakota Certified should be lower since these two genotypes were the highest in Δ during this period. When these two genotypes are omitted from the analysis, the relationship between WUE and Δ was negatively correlated ($r = -0.71$, $P \leq 0.05$, Fig. 1). During Days 5 to 8 of the drydown, WUE and Δ were not correlated during 2002

Table 2. Significance of variances and genotype means for evapotranspiration (ET), volumetric soil moisture content (VSMC) by soil depth, wilt, carbon-13 discrimination (Δ), and water use efficiency (WUE) at Days 5 to 8 during drydown (2002 and 2003).

	2002							2003					
		Change in VSMC by depth, cm							Change in VSMC by depth, cm				
	ET	17.5	35	52.5	Δ	WUE	Wilt†	ET	17.5	35	52.5	Δ	WUE
Source of variation							*P* values						
Blocks	***	*	*	ns‡	*	***	ns	***	***	***	ns	ns	ns
Genotype	***	*	*	§	***	§	*	§	ns	ns	ns	**	ns
Low vs. high¶	***	§	**	ns	***	ns	ns	ns	ns	ns	ns	**	*
Among low#	***	ns	ns	*	§	*	*	*	ns	ns	ns	§	ns
Among high#	**	*	§	ns	*	ns	ns	ns	ns	ns	ns	§	ns
							Genotype means						
Low water use	mm d^{-1}	$m^3\ m^{-3}$			‰	mg mL^{-1}	%	mm d^{-1}	$m^3\ m^{-3}$			‰	mg mL^{-1}
'Freedom'	5.2	3.0	3.0	3.4	20.71	0.07	34	6.3	2.7	2.4	4.9	21.07	0.10
'Indigo'	6.6	2.7	4.0	4.4	20.39	0.16	6	6.6	2.5	2.5	4.5	21.03	0.16
'Midnight'	7.0	2.7	4.0	4.8	20.32	0.13	3	7.6	2.5	2.5	4.3	20.94	0.15
'Nassau'	6.2	2.3	3.2	3.5	20.83	0.11	36	6.0	2.3	1.7	4.1	21.43	0.11
'Ram I'	5.8	3.1	3.4	3.7	20.58	0.09	19	7.0	2.8	2.5	4.4	20.83	0.10
'Suffolk'	5.4	2.9	3.3	3.5	20.58	0.10	18	6.2	2.5	2.4	4.8	20.99	0.11
Mean	6.0	2.8	3.4	3.9	20.57	0.11	19	6.6	2.5	2.3	4.5	21.05	0.12
High water use													
'Abbey'	6.3	3.5	3.5	3.8	20.99	0.08	23	6.5	2.5	2.0	4.7	21.57	0.11
'Eclipse'	6.0	2.9	3.7	3.9	20.62	0.10	18	6.9	2.4	2.3	4.3	21.13	0.11
'Ginger'	6.4	3.2	3.6	3.5	21.00	0.09	29	5.6	1.8	1.7	3.4	21.49	0.06
'Kenblue'	6.5	2.9	4.5	4.3	21.18	0.10	24	6.6	2.6	2.3	5.5	21.48	0.05
'Livingston'	6.7	2.5	4.0	4.2	20.65	0.13	10	7.2	2.1	2.6	4.6	21.08	0.10
'SD Certified'	7.6	3.0	4.4	4.4	20.80	0.15	6	6.8	2.9	2.6	3.9	21.22	0.12
Mean	6.6	3.0	3.9	4.0	20.87	0.11	18	6.6	2.4	2.3	4.4	21.33	0.09
LSD (0.05)	0.7	0.6	0.9	1.0	0.37	0.06	21	1.2	ns	ns	ns	0.42	0.07
CV, %	7.7	13.9	16.9	16.9	1.2	38.0	80.5	12.3	21.8	21.9	26.9	1.4	46.5

* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.
† Percentage of grass showing leaf fold, leaf roll, and blue-gray discoloration symptoms at Day 8 of drydown.
‡ ns = not significant.
§ Significant at the 0.1 level.
¶ Single df test for the difference between the combined means for low- vs. high-water-use genotypes.
\# Test for the differences within low-water use or high-water-use genotypes.

($r = -0.43$, $P > 0.10$, Fig. 1) but were negatively correlated in 2003 ($r = -0.52$, $P \leq 0.10$, Fig. 2).

According to theory, WUE and Δ are inversely related if the following assumptions are met (i) leaf-to-air vapor pressure (hence leaf temperatures) are constant across plants, and (ii) the fraction of carbon fixed during photosynthesis that is lost by respiratory processes do not vary (Farquhar and Richards, 1984). These assumptions may not be strictly met under all experimental conditions. Previous studies with Kentucky bluegrass (Ebdon et al., 1998a) have shown that leaf temperatures can vary considerably in the greenhouse, violating the constant leaf temperature assumption, thus reducing the predictive value of Δ for WUE.

Evapotranspiration and Rooting

Differences in ET rate among the 12 genotypes were detected at all periods during the 2002 and 2003 drydown (Tables 1, 2, 3, and 4). As soil moisture deficits progressed with soil drying in 2002, ET rates declined from 8.40 (Days 1 to 4) to 4.03 mm d^{-1} (Days 9 to 12). Similarly, in 2003, ET declined from 6.75 (Days 1 to 4) to 3.90 mm d^{-1} (Days 13 to 16). Water use rates among genotypes determined under nonlimiting soil moisture (Days 1 to 4) in 2002 and 2003 were uncorrelated with ET measured after this period under moisture-limited conditions. Therefore, ET measured under well-watered conditions was not necessarily a good predictor of water use under stress as suggested by Fernandez and Love (1993).

The six low-water-use genotypes had significantly lower ET rates than the high-water-use genotypes at all stages of the 2002 drydown (Tables 1, 2, and 3). However, in 2003, no difference between low- and high-water-use genotypes was detected after Day 4. Little to no difference within low- and high-water-use genotypes was detected under favorable soil moisture (Days 1 to 4) in 2002 and 2003 (Table 1). Differences in ET, especially among low-water-use genotypes, were more readily apparent in 2002 and 2003 only after soil moisture stress developed by Days 5 to 8 (Table 2) and as soil drying progressed into Days 9 to 12 (Table 3) and Days 13 to 16 (Table 4) of the drydown.

Genotypic differences in the change in VSMC by depth were dependent on the extent of soil drying and the severity of moisture stress. Generally, differences between genotypes at the 8.25-cm depth were only observed early in the drydown period (Days 1 to 4, Table 1). Conversely, changes in TDR-VSMC at greater depths (17.5, 35, and 52.5 cm) were only apparent later in the drydown during periods when tissue dehydration (wilt and leaf firing) was observed (Tables 2, 3, and 4). Changes in VSMC in the deepest part of the soil profile (35 and 52.5 cm) were positively correlated with ET rate ($P \leq 0.001$) in the 12 genotypes. These results suggest that Kentucky bluegrass genotypes exhibiting

Table 3. Significance of variances and genotype means for evapotranspiration (ET), volumetric soil moisture content (VSMC) by soil depth, wilt, and leaf firing at Days 9 to 12 during drydown (2002 and 2003).

	2002					2003			
		Change in VSMC by depth, cm					Change in VSMC by depth, cm		
	ET	17.5	35	52.5	Leaf firing†	ET	35	52.5	Wilt‡
Source of variation					*P* values				
Blocks	***	ns§	***	ns	ns	ns	ns	¶	ns
Genotype	***	¶	**	ns	*	*	ns	**	**
Low vs. high¶	*	*	***	ns	ns	ns	ns	ns	¶
Among low††	***	ns	ns	*	**	*	ns	**	**
Among high††	¶	*	ns	ns	ns	ns	ns	ns	ns
					Genotype means				
Low water use	mm d^{-1}		m^3 m^{-3}		%	mm d^{-1}	m^3 m^{-3}		%
'Freedom'	3.0	1.8	1.0	1.7	33	4.1	0.7	2.4	38
'Indigo'	4.6	1.7	1.6	2.7	9	4.4	0.9	3.3	43
'Midnight'	5.1	1.5	1.4	4.3	3	5.9	1.4	6.8	14
'Nassau'	3.7	1.7	1.0	1.5	30	3.3	0.5	2.3	70
'Ram I'	3.3	1.4	1.0	1.3	23	4.6	0.8	2.7	51
'Suffolk'	3.3	1.8	0.9	1.6	25	4.1	0.7	2.2	33
Mean	3.9	1.6	1.2	2.2	20	4.4	0.8	3.3	41
High water use									
'Abbey'	3.9	0.7	1.5	2.7	20	4.3	0.8	2.9	49
'Eclipse'	3.8	1.6	1.3	1.9	23	4.6	1.2	5.6	58
'Ginger'	4.0	1.5	1.7	2.0	24	3.2	1.1	1.9	55
'Kenblue'	4.1	1.2	1.5	2.0	19	4.2	1.0	2.5	55
'Livingston'	4.5	1.7	1.8	2.8	14	5.3	0.9	3.0	36
'SD Certified'	5.0	1.4	2.1	3.6	8	4.5	0.7	3.4	41
Mean	4.2	1.3	1.6	2.5	18	4.4	1.0	3.2	48
LSD (0.05)	0.8	0.7	0.6	2.0	17	1.4	ns	2.5	24
CV, %	14.5	30.9	30.9	59.3	62.5	22.2	71.6	53.4	37.4

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.001 level.

† Percentage of grass showing yellow, tan, and brown symptoms at Day 12 of drydown.

‡ Percentage of grass showing leaf fold, leaf roll, and blue-gray discoloration symptoms at Day 12 of drydown.

§ ns = not significant.

¶ Significant at the 0.1 level.

Single df test for the difference between the combined means for low- vs. high-water-use genotypes.

†† Test for the differences within low- or high-water-use genotypes.

greater rooting activity with depth were able to maintain higher ET with soil drying. Carrow (1996) concluded that deeper rooting and maintenance of ET were important for drought resistance in tall fescue.

Evapotranspiration and Rooting: Relationship to Drought Resistance

Significant differences between Kentucky bluegrass genotypes during the 2002 and 2003 drydowns were observed in wilting and leaf firing (Tables 2, 3, and 4). Visual estimates in 2002 for wilting ranged from 3 (Midnight) to 36% (Nassau), while leaf firing ranged from 3 (Midnight) to 33% (Freedom) (Tables 2 and 3). Wilting during the 2003 drydown ranged from 14 (Midnight) to 70% (Nassau) and leaf firing ranged from 12 (Midnight) to 73% (Nassau) (Tables 3 and 4). Year-to-year variations in genotype wilting tendency and leaf firing were positively correlated ($r = 0.64$ for wilt, $P \leq 0.05$; $r = 0.54$ for leaf firing, $P \leq 0.10$).

Perdomo et al. (1996) and others have suggested that low ET determined under well-watered conditions may not be appropriate for selecting turfgrass under limited soil moisture. Accordingly, genotypes of diverse ET were compared in this study to test the validity of the low ET model. In 2003, low-ET genotypes had significantly lower wilting tendency than high-ET genotypes (Table 3). No consistent pattern, however, was observed in wilting tendency or leaf firing during the 2002 or 2003 drydown between water use groups (low vs. high) (Tables 2, 3, and 4). These results do not necessarily support the low-ET concept, which suggests turfgrass possessing a more-conservative water use pattern determined under non-limiting soil moisture may be useful in selecting turfgrass for superior performance during drought. Furthermore, ET rates at Days 1 to 4 of the drydown were generally uncorrelated with wilt and leaf firing (Table 5). The exception occurred in 2003, where higher ET rates at Days 1 to 4 was associated with greater wilting by Day 12 ($r = 0.53$, $P \leq 0.10$). Therefore, ET under these conditions had little to no predictive value for turfgrass performance under drought.

During the 2002 and 2003 drydown, Midnight maintained significantly higher ET rates and less wilt and leaf firing than many of the low-water-use genotypes. Perdomo et al. (1996) also reported that Midnight maintained higher ET during summer stress in New Jersey, and this ability contributed to Midnight's superior summer performance. In Colorado field studies, Dernoeden and Butler (1978) observed higher drought resistance with common-type genotypes such as South Dakota Certified. Similarly, South Dakota Certified had significantly higher ET during the 2002 drydown compared with other high water use types, and was associated with

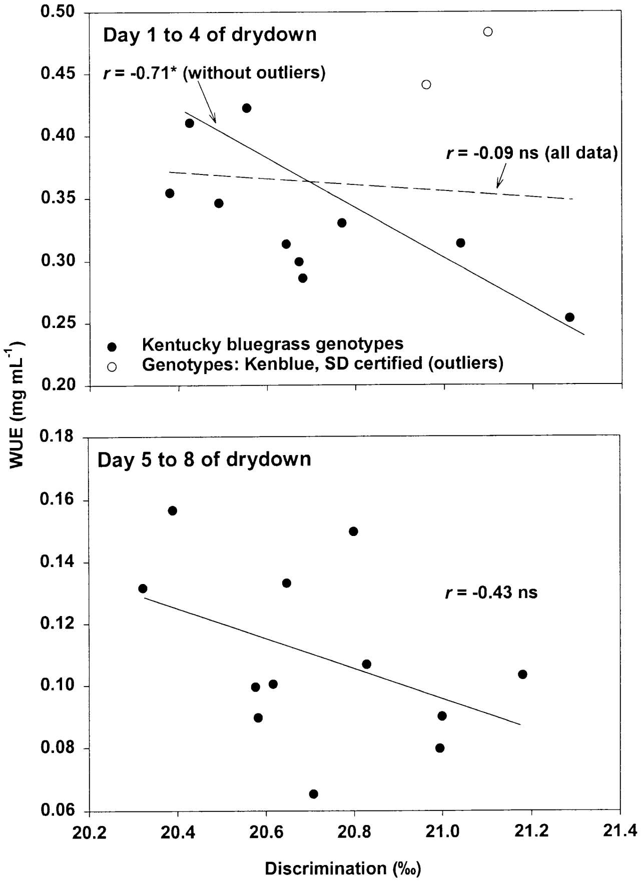

Fig. 1. Relationship between ^{13}C discrimination (Δ) and water use efficiency (WUE) among 12 Kentucky bluegrass genotypes at Days 1 to 4 and 5 to 8 during drydown in 2002. ns = nonsignificant at $P > 0.10$. *Significant at $P \leq 0.05$.

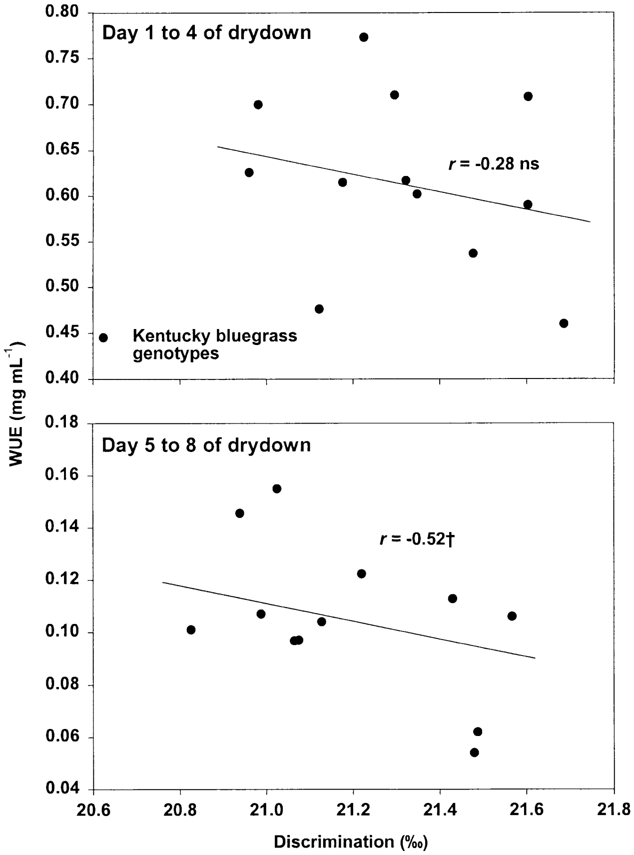

Fig. 2. Relationship between ^{13}C discrimination (Δ) and water use efficiency (WUE) among 12 Kentucky bluegrass genotypes at Days 1 to 4 and 5 to 8 during drydown in 2003. ns = nonsignificant at $P > 0.10$. † Significant at $P \leq 0.10$.

consistently lower wilt and leaf firing symptoms (Tables 2 and 3). In 2003, however, Livingston Kentucky bluegrass maintained higher ET compared with other high water use types and afforded less wilt and leaf firing (Tables 3 and 4). Keeley and Koski (2001) also reported that Livingston provided superior drought resistance in Colorado while common-type genotypes such as South Dakota Certified and Kenblue were among the poorest, which contradicts earlier reports by Dernoeden and Butler (1978). These studies indicate that direct comparisons can yield variable results because of the complexity of drought resistance.

Bonos and Murphy (1999) and Perdomo et al. (1996) found that Kentucky bluegrass genotypes tolerant of heat and drought during New Jersey summer stress periods were associated with the ability to exploit moisture in the deepest portions of the soil profile and maintained higher ET rates. Our data also indicate that those genotypes that extracted more moisture at the 35- and 52.5-cm depths and maintained higher ET rates during progressive soil drying were associated with less wilting and leaf firing (Table 5). Studies have indicated that low stomatal resistance (open stomates), greater transpirational cooling, and lower leaf temperatures during stress are critical to maintaining photosynthetic activity and green tissue (Bonos and Murphy, 1999; Huang and Gao, 1999; Perdomo et al., 1996). The ability of turfgrass to persist under moisture stress is not limited, however, to rooting or ET rate. Maintenance of a positive water balance (turgor) through physiological (osmotic) adjustments have also been suggested as mechanisms contributing to superior quality under stress (Perdomo et al., 1996; Qian and Fry, 1997).

Greater rooting activity indicated by greater changes in VSMC at the 52.5-cm depth at Days 9 to 12 of the 2002 drydown accounted for 88% (r^2) of the total variation in leaf firing ($r = -0.94$, Table 5). Also during the 2003 drydown, variations in VSMC at the 52.5-cm depth at Days 13 to 16 accounted for 64% (r^2) of leaf firing ($r = -0.80$, Table 5). Rooting activity at the 35-cm depth explained less of the total variation in the loss in green cover (Table 5). Generally, as drought stress increased in severity during drydown, the relative importance of deep rooting increased (Table 5). Marcum et al. (1995) reported that the average maximum rooting depth in 25 Zoysiagrass (*Zoysia japonica* Steud.) genotypes evaluated in the greenhouse explained more of the total variation in percentage green cover under severe drought stress (0% of ET, nonirrigated conditions) compared with moderate drought stress (irrigating at 35% of ET). Carrow (1996) observed greater root length density with soil depth in tall fescue (*Festuca arundinacea* Schreb.) was associated with less leaf firing and wilting. In the

Table 4. Significance of variances and genotype means for evapotranspiration (ET), volumetric soil moisture content (VSMC) by soil depth, and leaf firing at Days 13 to 16 during the 2003 drydown.

	ET	Change in VSMC by depth, cm		Leaf firing†
		35	52.5	
Source of variation		*P* values		
Blocks	ns‡	*	§	ns
Genotype	*	§	*	***
Low vs. high¶	ns	ns	ns	ns
Among low#	*	ns	ns	***
Among high#	ns	*	**	***
		Genotype means		
Low water use	mm d^{-1}	—— $\text{m}^3\ \text{m}^{-3}$ ——		%
‘Freedom’	3.9	1.1	5.5	31
‘Indigo’	3.8	1.3	4.7	44
‘Midnight’	5.3	1.8	8.0	12
‘Nassau’	2.9	0.7	3.1	73
‘Ram I’	4.2	1.4	5.7	34
‘Suffolk’	3.8	1.1	4.7	30
Mean	4.0	1.2	5.3	37
High water use				
‘Abbey’	3.7	1.2	5.1	38
‘Eclipse’	3.8	1.5	5.5	53
‘Ginger’	2.8	0.4	1.8	59
‘Kenblue’	3.9	1.1	5.4	41
‘Livingston’	4.8	1.6	8.9	26
‘SD Certified’	4.0	1.7	6.5	31
Mean	3.8	1.3	5.5	41
LSD (0.05)	1.3	0.8	3.4	23
CV, %	23.2	45.5	43.8	41.5

* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.
† Percentage of grass showing yellow, tan, and brown symptoms at Day 16 of drydown.
‡ ns = not significant.
§ Significant at the 0.1 level.
¶ Single df test for the difference between the combined means for low- vs. high-water-use genotypes.
\# Test for the differences within low-water use or high-water-use genotypes.

same field study, Carrow (1996) reported less leaf firing during drydown with higher ET rates. Our results also indicate that less leaf firing was associated with higher ET during the 2002 and 2003 drydown (Table 5). These studies indicate compelling evidence that the maintenance of ET through deep rooting is important when turf is under moisture stress.

Water Use Efficiency and Carbon Isotope Discrimination: Relationship to Drought Resistance

Higher WUE during the 2002 drydown was associated with less leaf firing and wilting tendency. The WUE measured at Days 5 to 8 under moisture limited conditions was negatively correlated with wilt ($r = -0.79$, $P \le 0.01$) and leaf firing ($r = -0.83$, $P \le 0.001$) (Table 5). Variations in WUE accounted for approximately 70% of the variation in leaf firing, which was comparable with rooting and ET in assessing turf performance under drought. The WUE at Days 1 to 4 under nonlimiting soil moisture was less compelling in assessing turf performance under moisture stress (Table 5). During 2003, WUE was not significantly correlated with either wilt or leaf firing except during Days 5 to 8 of the drydown when WUE and wilting tendency were negatively correlated (Table 5). The WUE measured as clipping yield-to-water loss ratio may not always be a reliable predictor of turf performance under drought; however, WUE measured under periods of moisture stress (Days 5 to 8 in this study) appears to be more reliable compared with WUE determined under nonlimiting soil moisture.

Table 5. Correlation coefficients (r) between drought symptoms (wilting, leaf firing), and evapotranspiration (ET), change in volumetric soil moisture content (VSMC) by depth, water use efficiency (WUE), and carbon-13 discrimination (Δ) among 12 Kentucky bluegrass genotypes during drydown (2002 and 2003).

	2002		2003	
Predictor	Wilting, Day 8	Leaf firing, Day 12	Wilting, Day 12	Leaf firing, Day 16
ET				
Days 1 to 4	−0.09	−0.16	0.53†	0.39
Days 5 to 8	−0.63*	−0.83***	−0.57*	−0.72**
Days 9 to 12	–	−0.93***	−0.73**	−0.81***
Days 13 to 16	–	–	–	−0.89***
VSMC, Days 1 to 4				
8.25 cm	0.11	0.05	0.54†	0.55†
52.5 cm	−0.72**	−0.82***	ns‡	ns
VSMC, Days 5 to 8				
17.5 cm	0.12	0.12	ns	ns
35 cm	−0.62*	−0.75**	ns	ns
52.5 cm	−0.82***	−0.94***	ns	ns
VSMC, Days 9 to 12				
17.5 cm	–	0.18	ns	ns
35 cm	–	−0.70*	ns	ns
52.5 cm	–	−0.90***	−0.46	−0.40
VSMC, Days 13 to 16				
35 cm	–	–	–	−0.73**
52.5 cm	–	–	–	−0.80**
WUE				
Days 1 to 4	−0.47	−0.56†	−0.24	−0.32
Days 5 to 8	−0.79**	−0.83***	−0.48†	−0.32
Δ				
Days 1 to 4	0.45	0.25	0.49†	0.55†
Days 5 to 8	0.59*	0.40	0.56†	0.58*

* Significant at the 0.05 level.
** Significant at the 0.01 level.
*** Significant at the 0.001 level.
† Significant at the 0.1 level.
‡ ns = Differences between genotypes for corresponding predictor were not significant at the 0.05 level.

Tissues collected at Days 5 to 8 of the drydown with low Δ values (high theoretical WUE) were associated with less wilting in 2002 ($r = 0.59$, $P \le 0.05$, Table 5) and 2003 ($r = 0.56$, $P \le 0.10$, Table 5). The Δ accounted for approximately 30 to 35% of the total variation in Kentucky bluegrass wilting. Similarly, Δ was positively correlated with leaf firing during the 2003 drydown ($r = 0.58$, $P \le 0.05$, Table 5) but Δ was uncorrelated with leaf firing in 2002 ($r = 0.40$, $P > 0.10$, Table 5). The ability to predict turf performance under drought (wilting and leaf firing) with ^{13}C analysis of leaves growing under nonlimiting soil moisture (Days 1 to 4) was less effective compared with Days 5 to 8 of the drydown (Table 5). Farquhar and Richards (1984) and Johnson et al. (1990) also observed a stronger relationship between Δ and WUE with increasing soil moisture stress. However, significant correlations between Δ and turf performance under drought were detected during the 2003 drydown from tissues collected during prestress periods (Days 1 to 4). Therefore, selecting for low Δ in turfgrass may identify populations with potentially lower wilting and leaf firing tendencies and superior performance under drought.

Ebdon et al. (1998a) point out some of the advantages to the use of Δ as a selection criteria for drought resistance such as ^{13}C analysis high repeatability and low CV (Tables 1 and 2). Although Δ was not a reliable predictor for WUE in our study, selecting for low Δ appears to show potential for identifying cool-season turfgrass for improved drought resistance. Conversely, selecting for low ET was not important in drought survival. To determine the reliability of Δ and WUE in turfgrass breeding programs, further research is needed, including (i) comparisons between leaf Δ vs. whole plant analysis of Δ and WUE, and (ii) comparative studies with gas-exchange WUE as suggested by Heitholt (1989).

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