Effects of Abscisic Acid on Drought Responses of Kentucky Bluegrass

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ABSTRACT. Abscisic acid (ABA) is an important hormone regulating plant response to drought stress. The objective of this study was to investigate effects of exogenous ABA application on turf performance and physiological activities of kentucky bluegrass (*Poa pratensis* L.) in response to drought stress. Plants of two kentucky bluegrass cultivars, 'Brilliant' (drought susceptible) and 'Midnight' (drought tolerant), were treated with ABA (100 μM) or water by foliar application and then grown under drought stress (no irrigation) or well-watered (irrigation on alternate days) conditions in a growth chamber. The two cultivars responded similarly to ABA application under both watering regimes. Foliar application of ABA had no effects on turf quality or physiological parameters under well-watered conditions. ABA application, however, helped maintain higher turf quality and delayed the quality decline during drought stress, compared to the untreated control. ABA-treated plants exposed to drought stress had higher cell membrane stability, as indicated by less electrolyte leakage of leaves, and higher photochemical efficiency, expressed as Fv/Fm, compared to untreated plants. Leaf water potential was not significantly affected, whereas leaf turgor pressure increased with ABA application after 9 and 12 d of drought. Osmotic adjustment increased with ABA application, and was sustained for a longer period of drought in 'Midnight' than in 'Brilliant'. The results suggested that exogenous ABA application improved turf performance during drought in both drought-sensitive and tolerant cultivars of kentucky bluegrass. This positive effect of ABA could be related to increased osmotic adjustment, cell turgor maintenance, and reduced damage to cell membranes and the photosynthetic system.

Water availability is becoming increasingly limited for irrigation. Prolonged drought stress due to insufficient rainfall or irrigation can be detrimental for plant growth (Aronson et al., 1987; Beard, 1973; 1989; Huang and Gao, 1999). Therefore, improving drought resistance of plants by means of cultural practices and breeding becomes imperative for water conservation and maintenance of plant growth in water-limiting environments. This requires better understanding of physiological and biochemical factors involved in plant adaptations to drought stress.

Plant hormones, such as abscisic acid (ABA), play an important role in the regulation of plant tolerance to various environmental stresses, particularly drought stress (Quarrie, 1989, 1993). Endogenous ABA levels increase when plants are subjected to drought stress (Cao et al., 2000; Conti et al., 1994; Harris and Outlaw, 1991; Henson et al., 1981; Ilahi and Dorffling, 1982; Ivanovic et al., 1992). ABA accumulation has been found to protect plants from drought damage by inducing stomata closure to reduce water loss via transpiration (Borel et al., 1997; Li et al., 2000) and increasing hydraulic conductance for water movement from roots to leaves (Ludewig et al., 1988; Zhang et al., 1995). ABA inhibits leaf growth and reduces transpirational area, and thus can reduce water loss (Alves and Setter, 2000; Carrow, 1996; Sharp et al., 1994). ABA has also been found to induce the expression of some genes, which results in cellular changes that confer an ability to maintain cell turgor and withstand the damaging forces associated with reduced water potential and desiccation (Bray et al., 1999; Lebreton et al., 1995).

Exogenous application of ABA has been reported to improve drought tolerance in various plant species such as maize (*Zea mays* L.) (Bochicchio et al., 1991), pepper (*Capsicum annuum* L.)

(Leskovar and Cantliffe, 1992), old jack pine (*Pinus banksiana* L.) (Rajasekaran and Blake, 1999), and *Tradescantia virginiana* L. (Franks and Farquhar, 2001). While the importance of ABA in drought regulation is widely recognized, information on how ABA affects drought resistance in turfgrasses is limited. Only a few studies on effects of ABA on turfgrass have been documented. Stahnke and Beard (1982) reported that exogenous application of ABA reduced transpiration of creeping bentgrass (*Agrostis pulastris* Huds.) by 59%. Jiang and Huang (2002) found drought injury in tall fescue (*Festuca arundinacea* L.) was alleviated with foliar ABA application, which paralleled the delayed induction of protein synthesis. Understanding physiological effects of ABA on drought responses of turfgrass would help gain insight on drought resistance mechanisms, and would be important for water conservation in turfgrass management.

The objectives of this study were to examine how exogenous ABA application affects drought responses of two kentucky bluegrass cultivars differing in drought resistance, and to investigate whether the effects of ABA are related to the regulation of water relations, membrane protection, and/or photosynthetic activity. A relatively drought tolerant cultivar, 'Midnight', and a drought susceptible cultivar, 'Brilliant', of kentucky bluegrass were selected based on our previous studies (Wang and Huang, 2001).

Materials and Methods

PLANT MATERIALS AND GROWTH CONDITIONS. Mature sods (15 cm in diameter and 2 cm deep) of both cultivars were collected from field plots at Adelphia Turfgrass Experiment Station, Rutgers University, New Jersey. Sods were washed free of soil before planting in 20-cm-diameter × 60-cm-deep polyvinyl chloride tubes filled with a mixture of sand and top soil (fine, montmorillonitic, mesic, aquic arquidolls) (1:2, v/v). Plants were grown in a greenhouse for 60 d and then transferred to growth chambers with a temperature of 22/16 °C (day/night), a 14-h photoperiod,

and photosynthetically active radiation of 600 mmol·m⁻²·s⁻¹. Grasses were well watered and maintained at the above conditions in the growth chambers for 15 d to allow adaptation to the growth-chamber conditions before drought treatment was imposed. Controlled-release fertilizer (17N–6P–10K) was top-dressed twice to provide N at 50 kg·ha⁻¹ prior to drought treatment. Turf was hand clipped twice weekly at a 6-cm height.

EXPERIMENTAL DESIGN AND TREATMENTS. For ABA treatment, 40 mL of (±) ABA (100 μM) solution were sprayed uniformly on a 0.32 m² of foliage using a spray bottle at 1000 HR once daily for a 3-d period before soil moisture treatments were initiated. A total of 3.3 mg (±) ABA was applied per square meter turf area. The cost to treat the turf with ABA at the rates used in this study is about \$0.033/m² turf area based on the price of a commercial (+)ABA analog (S-ABA, \$20/g, Lomon Bio Technology, Chengdu, China). Plants untreated with ABA were sprayed with 40 mL of deionized water. Both ABA-treated and untreated plants were exposed to two moisture regimes.
A) Drought stress: irrigation was withheld for 30 d.
B) Well-watered control: plants were irrigated every other day until drainage occurred from the bottom of the pot.

The experiment was a completely randomized design, with factorial arrangement (soil moisture, ABA, and cultivars). Each treatment had four replicates.

MEASUREMENTS. Volumetric soil water content in 0 to 20 cm soil layer was monitored to determine soil dryness during drought stress by time domain reflectometry (TDR, Soil Moisture Equipment Corp., Santa Barbara, Calif.). The field capacity of the sand and topsoil mix was 26.8% ± 0.5% (mean of eight replications ± SE), which was measured in 8 pots with TDR when drainage ceased following watering the soil to complete saturation. Soil water content declined to 15% by 12 d and 5% by 30 d of drought.

Several physiological measurements were made at 6-d intervals during the experiment. Turf quality was rated visually on the basis of color, uniformity, and density on a 0 to 9 scale where 0 = worst quality, 6 = minimum acceptable quality, and 9 = best quality. Vertical shoot extension rate was estimated by measuring the difference in the mean canopy height in 2-d intervals. The first and second youngest, fully expanded leaves from different plants in each pot were sampled to measure leaf water potential, osmotic potential, electrolyte leakage, and sugar content. Leaf water potential and osmotic potential were measured using a thermocouple psychrometer (Decagon Devices, Inc., Pullman, Wash.). Leaf turgor was calculated as the difference between leaf water potential and osmotic potential. Osmotic adjustment was calculated as the difference in osmotic potential at full turgor ($\Psi_{\pi100}$) between control and stressed plants ($\Psi_{\pi0}$) (Blum, 1989; Blum and Sullivan, 1986). Cell membrane stability was estimated by measuring electrolyte leakage (EL). A 0.1 g sample of leaves was rinsed and immersed in 20 mL of deionized water. The conductivity of the solution ($C_{initial}$) was measured after the leaves were shaken for 24 h. Leaves were then killed by autoclaving at 140 ºC for 20 min. The conductivity of killed tissues (C_{max}) was measured after samples were cooled to room temperature. Relative EL was calculated as the percentage of $C_{initial}$ over C_{max}. Leaf photochemical efficiency, expressed as the ratio of variable fluorescence to the maximum fluorescence (Fv/Fm) of chlorophyll, was determined weekly on 4 leaves in each pot with a fluorescence induction monitor (Dynamax, Houston, Texas).

The content of water soluble sugars was determined following the method described in Buysse and Merckx (1993). Fifty milligram of dry leaf powder was extracted with 80% (v/v) ethanol for

three times (20 mL). The total volume of the combined and filtered extracts was adjusted to 100 mL using deionized water. One milliliter of samples was transferred into a glass tube, and 1 mL 18% (w/v) phenol solution was then added. Immediately afterwards, 5 mL of concentrated sulphuric acid were added, the solution in the tube was mixed using a vortex mixer. Tubes were allowed to stand for 20 min and cooled down to room temperature before absorbance was measured with a spectrophotometer at 490 nm (Genesys, Spectronic Instruments, Inc., Rochester, N.Y.).

STATISTICAL ANALYSIS. Effects of ABA, soil moisture, cultivar, and their interactions were determined using an analysis of variance according to the general linear model procedure of Statistical Analysis System (SAS Institute, Cary, N.C.). Each treatment mean was the average of four replications. Effects of ABA for each cultivar were analyzed by comparing to their respective untreated controls under well-watered or drought stress conditions at a given time of treatment. Differences among treatments and cultivars were determined by Tukey's studentized range test using the minimum significance difference (MSD) at the 0.05 probability level.
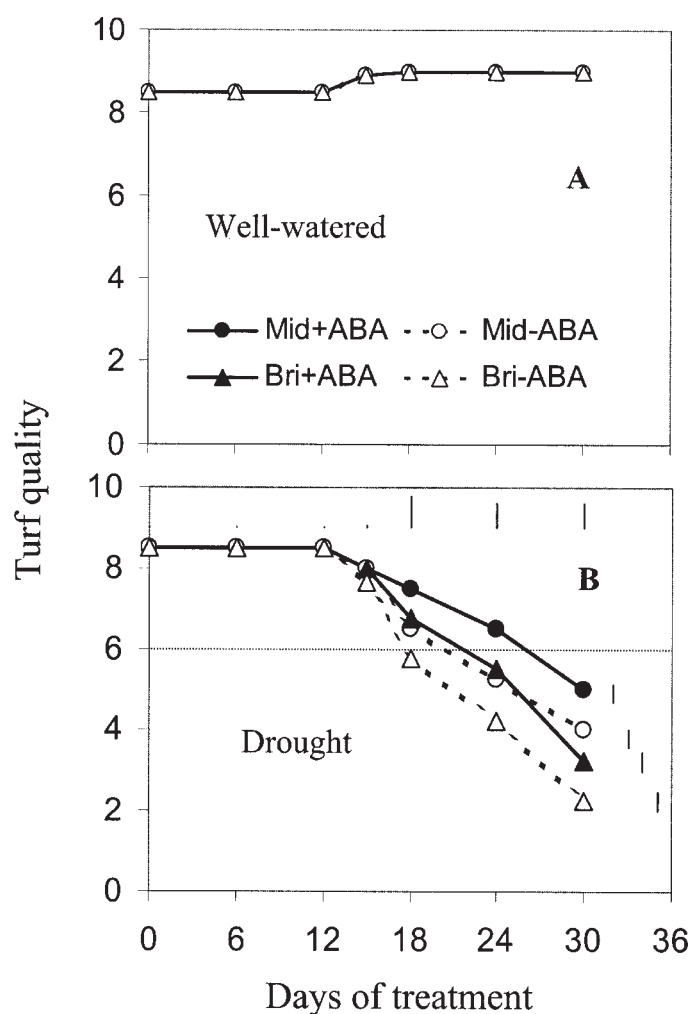

Fig. 1. Effects of ABA on turf quality in two kentucky bluegrass cultivars under well-watered (**A**) and drought (**B**) conditions. Mid+ABA: 'Midnight' with ABA application; Mid-ABA: 'Midnight' without ABA treatment; Bri+ABA: 'Brilliant' with ABA treatment; Bri-ABA: 'Brilliant' without ABA treatment. Vertical bars on the top indicate MSDs (*P* = 0.05) for treatment comparison at a given day of drought. Vertical bars on the right indicate MSDs (*P* = 0.05) for turf quality comparison over time within the treatment.

Results

TURF QUALITY. ABA application had no effect on turf quality in well-watered plants of either 'Brilliant' or 'Midnight' (Fig. 1A). Turf quality started to decline below the initial control level at 15 d of drought stress in both ABA-treated and untreated plants for both cultivars, and to below the minimum acceptable level (6.0) at 18 d for untreated 'Brilliant' and 24 d for untreated 'Midnight' (Fig. 1B). ABA application delayed the decline and maintained a better turf quality than untreated controls for both cultivars at 18, 24, and 30 d of drought stress. 'Midnight' exhibited higher quality than 'Brilliant' after 18 d of drought for both ABA-treated and untreated plants.

SHOOT GROWTH RATE. Vertical shoot extension rate of ABA-treated plants was less than that of the untreated plants for both cultivars only at 6 d of ABA application under well-watered conditions, but the growth rate recovered to the untreated level afterward (Fig. 2A). Shoot growth rate of both cultivars declined rapidly with drought (Fig. 2B). ABA application had no significant effects on shoot growth rate for either cultivar under drought conditions.
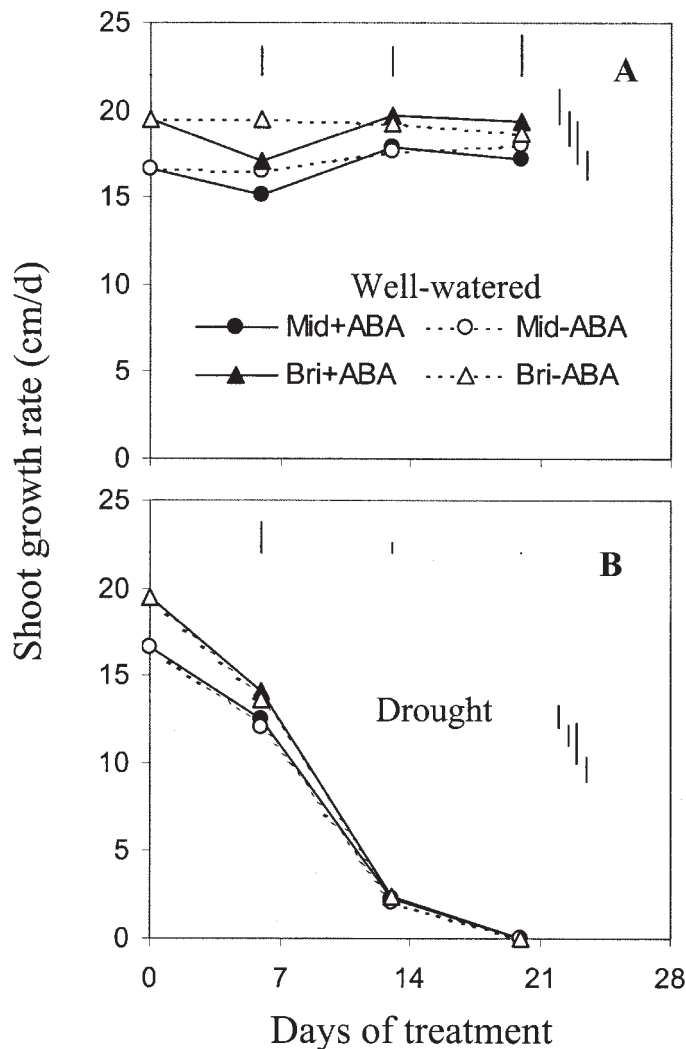
ELECTROLYTE LEAKAGE. Electrolyte leakage (EL) was not affected by ABA application under well-watered conditions (Fig. 3A). Under drought conditions, however, ABA application reduced EL in both cultivars, to a greater extent for 'Brilliant' than for 'Midnight' at 18, 24, and 30 d of treatment (Fig. 3B). During drought stress, EL of 'Brilliant' increased sharply above the initial level at 12 d, while EL of 'Midnight' did not show a significant increase until 24 d of stress in both ABA treated and untreated plants. 'Midnight' had lower EL than 'Brilliant' in either ABA-treated or untreated plants after 18 d of drought.

PHOTOCHEMICAL EFFICIENCY (F_v/F_m). No difference in F_v/F_m ratio was detected between cultivars and ABA applications under well-watered conditions (Fig. 4A). Drought stress caused a significant decline in F_v/F_m ratio, beginning 18 d for 'Brilliant' and 24 d for 'Midnight' in ABA-untreated plants (Fig. 4B). The decline in the F_v/F_m ratio was greater for 'Brilliant' than for 'Midnight'. ABA application delayed the decline of F_v/F_m ratio during drought stress and maintained a higher F_v/F_m ratio than the untreated control, for both cultivars, especially for 'Brilliant' at 18 d of stress (Fig. 4B).
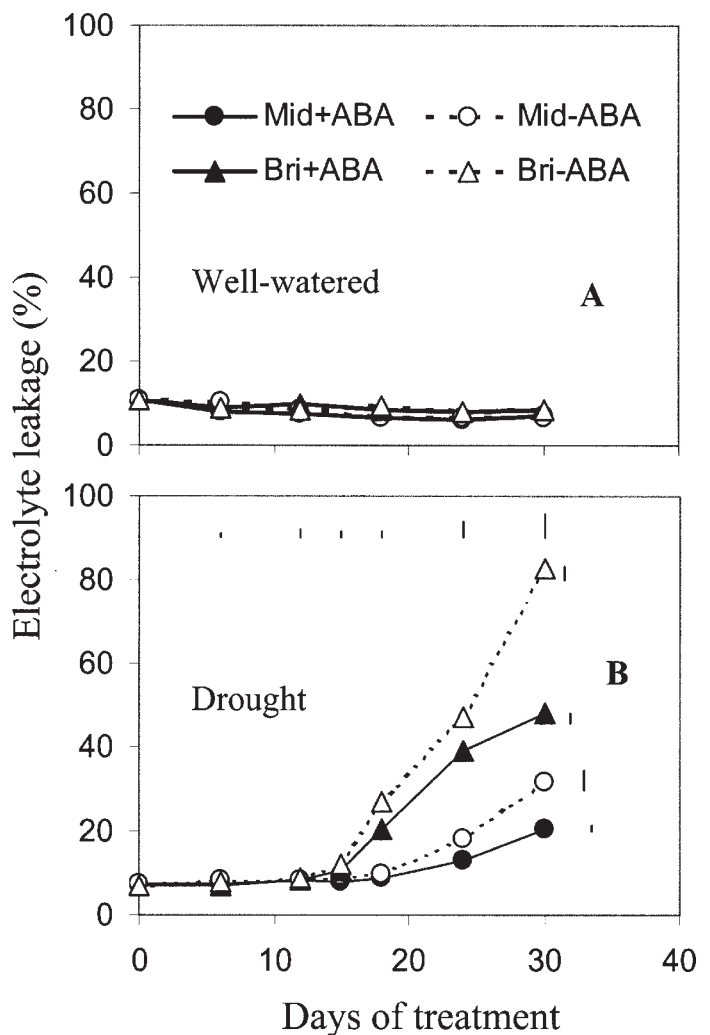

Fig. 2. Effects of ABA on shoot growth rate in two kentucky bluegrass cultivars under well-watered (**A**) and drought (**B**) conditions. Mid+ABA: 'Midnight' with ABA application; Mid-ABA: 'Midnight' without ABA treatment; Bri+ABA: 'Brilliant' with ABA treatment; Bri-ABA: 'Brilliant' without ABA treatment. Vertical bars on the top indicate MSDs ($P = 0.05$) for treatment comparison at a given day of drought. Vertical bars on the right indicate MSDs ($P = 0.05$) for comparison over time within the treatment.

Fig. 3. Effects of ABA on leaf electrolyte leakage in two kentucky bluegrass cultivars under well-watered (**A**) and drought (**B**) conditions. Mid+ABA: 'Midnight' with ABA application; Mid-ABA: 'Midnight' without ABA treatment; Bri+ABA: 'Brilliant' with ABA treatment; Bri-ABA: 'Brilliant' without ABA treatment. Vertical bars on the top indicate MSDs ($P=0.05$) for treatment comparison at given day of treatment. Vertical bars on the right indicate MSDs ($P=0.05$) for electrolyte leakage comparison over time within the treatment.
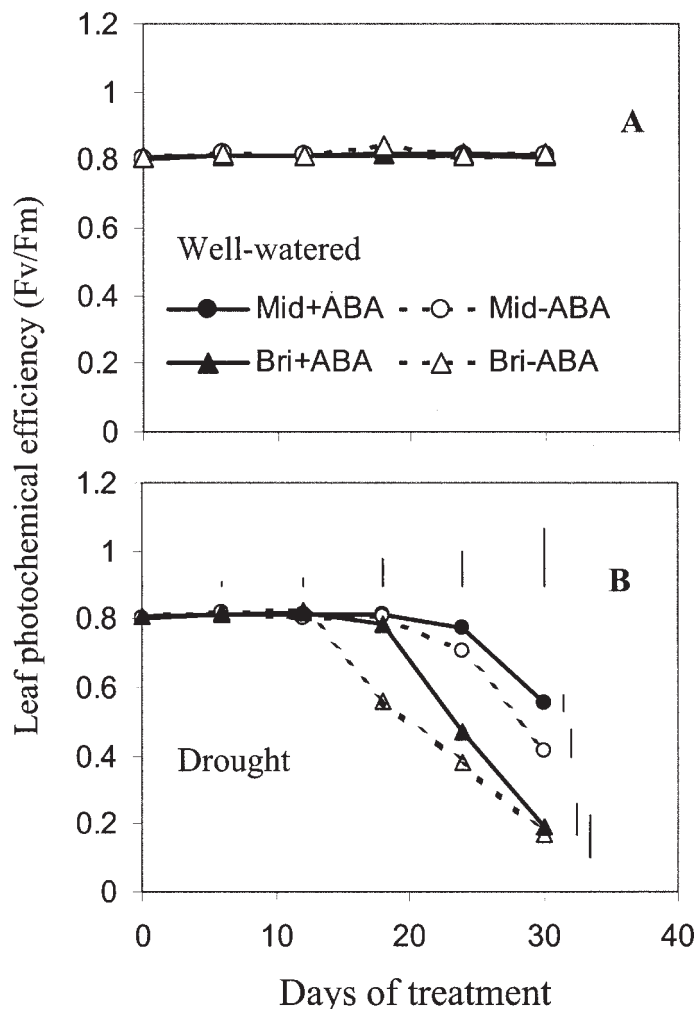
Fig. 4. Effects of ABA on leaf photochemical efficiency in two kentucky bluegrass cultivars under well-watered (**A**) and drought (**B**) conditions. Mid+ABA: 'Midnight' with ABA application; Mid-ABA: 'Midnight' without ABA treatment; Bri+ABA: 'Brilliant' with ABA treatment; Bri-ABA: 'Brilliant' without ABA treatment. Vertical bars on the top indicate MSDs ($P = 0.05$) for treatment comparison at a given day of treatment. Vertical bars on the right indicate MSDs ($P = 0.05$) for Fv/Fm ratio comparison over time within the treatment.

WATER RELATIONS. Leaf water potential (Ψ_{leaf}) and leaf turgor pressure (Ψ_p) of both cultivars declined with drought stress (Table 1). The decline for both Ψ_{leaf} and Ψ_p was greater for 'Brilliant' than 'Midnight'. ABA application increased Ψ_{leaf} at 12 d of drought for 'Midnight' and 9 d for 'Brilliant', but had no significant effects on Ψ_{leaf} at others days of drought for both cultivars. ABA application helped maintain higher Ψ_p at 9 and 12 d of drought for 'Midnight' and 6, 9, and 12 d for 'Brilliant'.

ABA application increased osmotic adjustment (OA) of both cultivars during drought stress compared to their respective, untreated controls (Fig. 5A and B). Increased OA with ABA exhibited at 4, 6, and 12 d of drought for 'Brilliant' (Fig. 5A) and 12, 18, 24, and 30 d for 'Midnight' (Fig. 5B).

SOLUBLE SUGAR CONTENT. Water soluble sugar content increased with drought progression, beginning at 18 d for 'Brilliant' and 24 d for 'Midnight' (Fig. 6). The increases were less pronounced for ABA-treated than untreated plants for both cultivars. ABA-treated plants had higher soluble sugar content than untreated plants at 6 d of treatment in both cultivars under both well-watered (Fig. 6A) and drought conditions (Fig. 6B), but lower soluble sugar content at 18, 24, and 30 d of drought.

Discussion

Cultivars generally did not differ in their responses to ABA application, although 'Midnight' was more tolerant to drought than 'Brilliant', as indicated by its higher turf quality, Ψ_{leaf}, Fv/Fm ratio, and lower EL. Exogenous ABA application improved turf quality, but had no significant effect on shoot growth rate for either 'Midnight' or 'Brilliant' under prolonged drought stress. Shoot growth ceased after 18 d of drought stress for both ABA-treated and untreated plants.

ABA application suppressed the increases in EL and the decline in Fv/Fm, suggesting that ABA could reduce drought injury by protecting cell membrane and photosynthesis apparatus. Rajasekaran and Blake (1999) reported that old jack pine seedlings treated with ABA maintained a higher photosynthetic rate and had lower EL than untreated plants. They found that the protective action of ABA on membrane integrity was associated with an inhibition of ethylene evolution during drought stress. Another protective process induced by ABA is the synthesis of dehydrin proteins (Bray, 1993; Chandler and Robertson, 1994; Close, 1996; Landi et al., 2001). These protective proteins can enhance water binding and ion-sequestering properties that allow them to interact with enzymes and other cell constitutes in such a way that their critical functions are preserved during drought stress (Campalans et al., 1999; Cellier et al., 1998; Lorenzo et al., 2001; Neill and Burnett, 1999; Tamminen et al., 2001; Wood and Goldsbrough, 1997). Jiang and Huang (2002), however, found that ABA-enhanced drought tolerance was not related to the induction of dehydrin in tall fescue, but increased water retention.

Osmotic adjustment facilitates the maintenance of water re-

Table 1. Effects of ABA on leaf water potential and turgor pressure under drought conditions.

Days of drought	Leaf water potential (MPa)				Turgor pressure (MPa)			
	Midnight		Brilliant		Midnight		Brilliant	
	+ABA	−ABA	+ABA	−ABA	+ABA	−ABA	+ABA	−ABA
0	−0.82 a[z]	−0.82 a	−0.70 a	−0.70 a	0.86 b	0.86 b	1.09a	1.09 a
6	−0.88 a	−0.91 a	−0.80 a	−0.89 a	1.04 a	1.09 a	1.06 a	1.12b
9	−0.90 a	−1.12 a	−0.86 a	−1.13 b	0.95 a	0.76 b	1.16 a	0.99b
12	−1.31 a	−1.57 b	−2.02 a	−2.05 a	0.57 a	0.45 b	0.15 a	0.037b
16	−2.02 a	−2.07 a	−2.58 a	−2.86 a	0.00	0.00	0.00	0.00
MSD	0.33	0.38	0.46	0.32	0.11	0.19	0.18	0.17

[z]Means followed by the different letters within a row indicate significant differences between +ABA and −ABA treatments for a given cultivar based on Tukey's test of MSD at $P = 0.05$. The MSD values ($P = 0.05$) were for the comparison over time within +ABA or −ABA treatment.

tention and cell turgor through accumulation of organic or inorganic solutes (Guicherd et al., 1997; Ranney et al., 1991; Wang et al., 1995; Zhang and Archbold, 1993), thus protecting tissues from desiccation as water potentials decrease (Bohnert et al., 1995; Bray, 1993). ABA application enhanced osmotic adjustment in both kentucky bluegrass cultivars, but increased OA with ABA were sustained for a longer period of drought for drought-tolerant 'Midnight' than sensitive 'Brilliant'. This result suggests that enhanced OA with ABA could be a critical factor in regulating drought tolerance of kentucky bluegrass. This could contribute to the higher turgor pressure of leaves treated with ABA compared to those of untreated leaves in both cultivars. Enhanced plant tolerance associated with ABA to salinity stress has been related to the stimulation of osmotic adjustment in *Phaseolus vulgaris* L. (Cachorro et al., 1995).

Water soluble sugars have been found to be associated with osmotic adjustment in response to water stress in some plant species (Munns and Weir, 1981; Ranney et al., 1991; Tan et al., 1992; Zhang and Archbold, 1993). In the present study, ABA application induced a significant increase of soluble sugar con-

tent only at 6 d in both well watered and drought conditions. Under prolonged and severe drought stress conditions, soluble sugar content, however, was higher in untreated than ABA-treated plants and in the drought sensitive cultivar than in the tolerant cultivar. Therefore, increased osmotic adjustment during prolonged, severe drought was not related to soluble sugar accumulation in this study, which could be due to accumulation of other solutes. Barathi et al. (2001) found that increases in soluble sugar content during prolonged drought stress was accompanied by decreases of starch, proteins, and nucleic acids, which indicates drought injury. In the present study, increases in soluble sugar content occurred after 18 d of drought for 'Brilliant' and 24 d for 'Midnight' when soil water was nearly depleted, which was coincident with the increases in EL and decreases in turf quality, indicating that soluble sugar increase in this stage could be associated with cell damage and leaf senescence.

In conclusion, exogenous application of ABA improved drought tolerance for both cultivars of kentucky bluegrass in our controlled environment study. The enhanced drought tolerance could result from increased cell membrane stability and photochemical
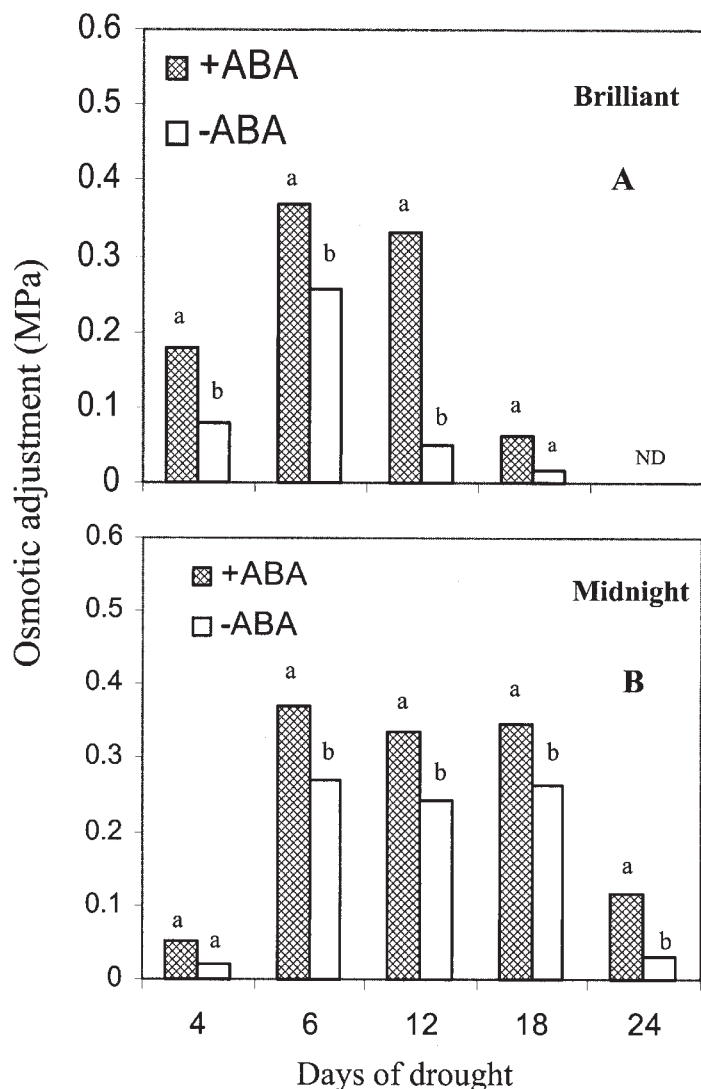
Fig. 5. Effects of ABA on osmotic adjustment under drought stress in two kentucky bluegrass cultivars. Columns marked with different letters indicate a significant difference between ABA-treated and untreated plants at a given day of treatment (MSD at $P = 0.05$).
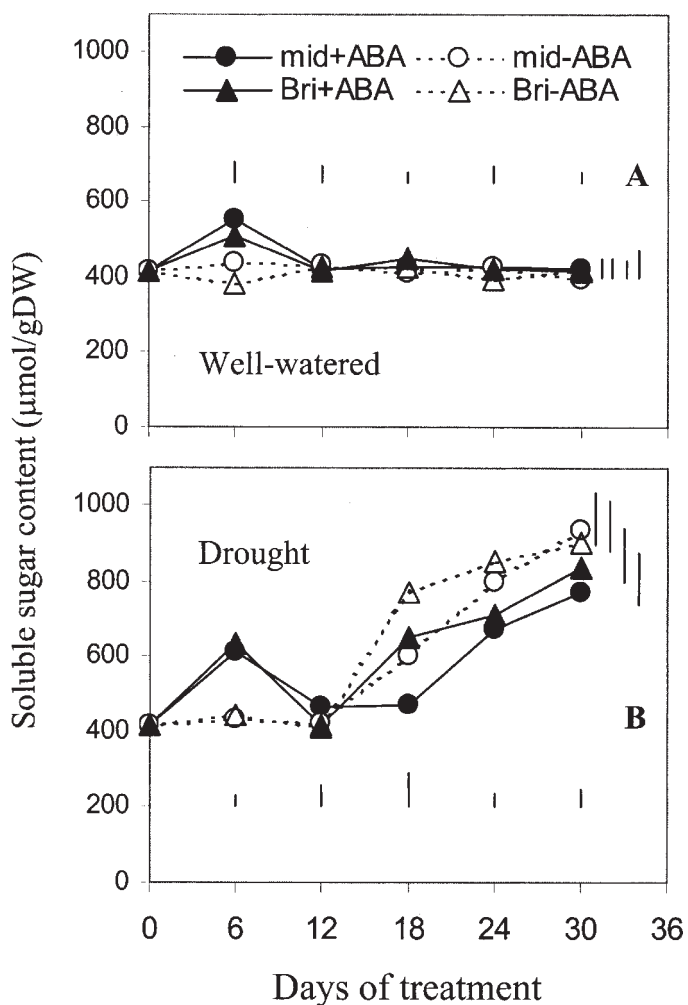

Fig. 6. Effects of ABA on water-soluble sugar content in two kentucky bluegrass cultivars under well-watered (**A**) and drought (**B**) conditions. Mid+ABA: 'Midnight' with ABA application; Mid-ABA: 'Midnight' without ABA treatment; Bri+ABA: 'Brilliant' with ABA treatment; Bri-ABA: 'Brilliant' without ABA treatment. Vertical bars on the top indicate MSDs ($P = 0.05$) for treatment comparison at a given day of treatment. Vertical bars on the right indicate MSDs ($P = 0.05$) for soluble sugar comparison over time within the treatment.

efficiency, and turgor maintenance associated with osmotic adjustment. Field research is in progress to confirm the effects of ABA on drought tolerance in several turfgrass species under natural environmental conditions.

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