Heat Resistance Enhanced by Trinexapac-Ethyl and Benzyladenine Combination in Creeping Bentgrass

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Creeping bentgrass (*Agrostis stolonifera* var. *palustris* Huds) is one of the most widely used turfgrasses for golf greens and fairways. The optimum temperature for creeping bentgrass ranges between 15 to 24 °C for shoot growth and 10 to 18 °C for root growth (Beard, 1973). However, temperatures during summer months often exceed the optimal ranges for prolonged periods. High-temperature stress is one of the major factors limiting use of creeping bentgrass in transitional and warmer climatic regions (Beard, 1997; Beard and Daniel, 1966; Carrow, 1996; Wang et al., 2003). Typically, grasses are exposed to high temperatures more than 35/30 °C (day/night) for 20 to 30 d during the summer in many areas of China. Such prolonged high temperatures severely limit shoot and root growth, and survival of plants.

Many physiological factors are involved in heat stress injury. Heat stress reduces photosynthesis (Carrow and Duncan, 2003; Paulsen, 1994; Xu and Huang, 2001), and increases respiration, which exhausts carbohydrate reserves (Xu and Huang, 2003). Carbohydrate metabolism is among the key physiological processes controlling plant growth. High-quality turf is often cultivated under a frequent mowing program. Clipping removal is one of the main concerns in reduction of energy reserves and leaf area required for photosynthesis in creeping bentgrass. Trinexapac-ethyl (TE) is a plant growth regulator that inhibits gibberellin (GA) synthesis by blocking the transforma-

tion of GA20 to GA1 (Rademacher, 2000). TE reduces vertical growth of many turfgrass species, which results in decreased clipping weights (Fagerness et al., 2004; McCullough et al., 2004; Tegg and Lane, 2004). TE has been shown to reduce sod heating through reducing plant respiration, resulting in enhanced stress resistance in Kentucky bluegrass (*Poa pratensis*) (Ervin and Koski, 2001a,b; Heckman et al., 2001), indicating its effects on energy conservation from respiratory consumption.

Cytokinin, a phytohormone, may regulate plant response to high-temperature stress. A period of heat stress reduced the level of cytokinins in roots in many plants (Itai et al., 1973; Liu et al., 2002; Udomprasert et al., 1995). Application of cytokinins (Liu and Huang, 2002) or products containing cytokinins (Zhang et al., 2003) to the root system or shoot (Zhang and Schmidt, 2000) could enhance the heat resistance of turfgrasses. The positive effects of cytokinins on stress resistance of plants are related to protection from oxidative stress by preventing the formation of free radicals or by the regulation of antioxidant enzyme activities (Caers et al., 1985; Liu and Huang, 2002; Wang et al., 2003; Zhang and Schmidt, 2000).

Although many plant growth regulators are commercially available for regulating plant growth and production, few of them have been reported to have positive effects on improving plant heat resistance. Cytokinins and TE are two chemicals that have shown potential beneficial effects for plant heat resistance in previous reports. However, no work has been conducted to determine the interactive effects of TE and 6-benzyladenine (BA). The objectives of this study were to investigate 1) whether a TE and cytokinin combination can enhance heat resistance of creeping bentgrass and 2) the morphological and physiological effects of TE and BA in the regulation of turf summer performance and heat resistance in creeping bentgrass.

Materials and Methods

Plant materials and growth conditions. Creeping bentgrass cultivar Penncross was seeded (6 g·m⁻²) in a 20-cm-diameter × 30-cm deep plastic pots filled with a mixture of sand and peatmoss (Pindstrup Sphagnum Peatmoss, specially for golf course use; 4 sand : 1 peatmoss, v/v) following the recommendation for green construction of the United States Golf Association (U.S. Golf Association Green Section staff, 1993). The plants were grown for 6 months under greenhouse conditions at 20/15 °C (day/night). Plants were mowed at a 1-cm height twice a week using electric clippers, watered daily, and fertilized weekly with 500 mL half-strength Hoagland's solution (Hoagland and Arnon, 1950). One week before the experiment, all pots were transferred to growth chambers at 20/15 °C with 600 μmol·m⁻²·s⁻¹ photosynthetically active radiation for a 14-h photoperiod.

Experimental design and treatments. Plants were treated with one of three chemical treatments of 40 mL in three foliar sprayings (2-h interval) in a night of TE 40 mg·L⁻¹ (0.51 kg·ha⁻¹), BA 50 mg·L⁻¹ (0.64 kg·ha⁻¹), and 40 mg·L⁻¹ TE + 50 mg·L⁻¹ BA. The concentrations of solutions were chosen based on a preliminary experiment (data not shown) for maximum effects on thermotolerance. The control plants were irrigated with 40 mL deionized water. Eight days after chemical treatments, plants were exposed to heat stress at 35/30 °C (day/night) for 24 d. During the heat stress period, plants were sprayed with 200 mL water per pot daily to avoid excess water loss of plant tissues.

Measurements. Measurements were made at 4-d intervals during the experiment. Turf quality was rated visually on the basis of color, uniformity, and density on a scale of 1 to 9 points where 1 point is worst quality, 6 points is minimum acceptable quality, and 9 points is best quality, according to National Turfgrass Evaluation Program Scale (USA). Shoot density was represented by tiller numbers on 1-cm² ground surface area.

Shoot growth rate was measured by the average turf canopy height grown above the previous mowing level in the 4-d interval. Clippings from each pot were collected for clipping yield. Fifty milligrams of fresh clippings were used for chlorophyll analyses, with the remaining clippings dried at 85 °C for 36 h for use in total nonstructural carbohydrate (TNC) analyses. Dry samples of clippings were ground with a tissue grinder and stored in sealed vials for TNC measurement.

Chlorophyll concentrations were measured according to the method of Arnon (1949). Fresh leaf samples (0.05 g) were cut into small pieces and extracted in dimethyl sulfoxide for 48 h in darkness. Extractions were measured for chlorophyll concentration with a spectrophotometer at 645 nm and 663 nm.

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TNC was measured using the method described by Smith (1981). Briefly, 50-mg oven-dried samples were hydrolyzed with 10 mL 0.1% clarse for 24 h at 37 °C. Then, 5 mL enzyme hydrolysis solution was hydrolyzed further with 0.6 mol·L⁻¹ HCl for 18 h at 22 °C. The HCl hydrolysis solution was adjusted to pH 5 to 7 with 10 M NaOH. One milliliter of the solution was then transferred to a 100-mL flask, and 5 mL ferricyanide reagent was added. Then the flasks were placed in a boiling water bath for 10 min. After heating, the flasks were cooled quickly in running water. The solution was neutralized partially with 10 mL 1 M H₂SO₄ solution and mixed thoroughly until no gas was evolved. Four milliliters of arsenomolybdate was added, and the solutions were mixed again and then diluted to volume. The absorbance of the solution was measured at 515 nm using a spectrophotometer (Jenway 6505, Essex, UK).

Statistical analysis. The experiment was a completely randomized design with four replicates. Effect of chemical pretreatment was determined using analysis of variance according to the general linear model procedure of the Statistical Analysis System (SAS Institute, Cary, N.C.). Each treatment mean was the average of four replicates. Differences among treatment means were determined using Fisher's LSD ($\alpha = 0.05$).

Results

Turf quality. Chemical treatments did not have significant effects on turf quality during 8 d before heat stress. Turf quality declined with the progression of the heat stress for all plants (Fig. 1). However, the combination of TE and BA treatment exhibited a delay in turf quality decline, followed by single TE or BA treatments. The turf quality of the TE + BA treatment was significantly higher than the

Fig. 1. Effects of trinexapac-ethyl (TE) and cytokinin on turf quality of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. The line at turf quality 6 shows the accepted turf quality level. BA, 6-benzyladenine; Ctrl, control.

control plants during the 24-d heat stress period. The TE treatment had a higher turf quality than the control after 8 d of heat stress. These two treatments maintained the turf quality above the acceptable level (>6) until 12 d of heat stress, compared only 4 d in the control plants. There were no significant differences in turf quality between the TE + BA and TE treatments except at 20 d and 24 d of heat stress. BA treatment alone had minor effects on turf quality when compared with TE + BA and TE treatments, but also maintained the turf quality above the acceptable level for 8 d under heat stress and showed significantly higher turf quality than the control at 8, 16, and 24 d.

Shoot density. TE + BA significantly increased tiller density for 8 d before heat stress (Fig. 2). However, after heat stress was imposed, TE + BA and TE treatments slowed the decline in density, followed by the BA treatment compared with controls. TE + BA and TE treatments exhibited significant higher tiller density than the control during the entire period of heat stress. No statistical difference was detected between TE + BA and TE treatments. BA treatment had less effect on shoot density than TE + BA and TE treatments, but showed a significantly higher shoot density than the control at 12 d.

Shoot growth rate and clipping yield. TE + BA and TE treatments inhibited shoot growth rate for 8 d before heat stress. When plants were exposed to heat stress for 4 d, the rate of shoot growth for the control increased 160% relative to the initial rate, followed by a sharp decline below to the initial level after 12 d of heat stress (Fig. 3). TE + BA, TE, and BA treatments suppressed the initial increases in shoot growth to 30%, 50%, and 74% at 4 d respectively. TE + BA and TE treatments maintained the shoot growth rate above the initial level until 20 d under heat stress. TE + BA-treated plants maintained a higher shoot growth rate than TE at 24 d. Compared with the control, BA maintained a higher shoot growth after 12 d of heat stress. But by 20 d and 24 d, shoot growth was similar to controls.

Clipping yield showed the same patterns as the shoot growth rate in response to heat stress (Fig. 4). Clipping yield of control plants increased during the first 8 d of heat stress, but decreased below to the initial level after 12 d. Clipping yield in TE + BA-, TE-, and BA-treated plants was much less than the control at 4 d of heat stress but maintained higher clippings for 20 d after heat stress compared with controls.

Chlorophyll concentration. TE + BA treatment increased leaf chlorophyll concentration during the 8 d before heat stress. After to exposure heat stress, leaf chlorophyll concentration showed steady declines for control and treated plants (Fig. 5). Control plants exhibited most rapid decline and had the lowest chlorophyll concentration among the four treatments. Under heat stress, chlorophyll concentration was highest in the TE + BA treatment, followed by TE- and BA-alone treatment. Compared with the control, BA

Fig. 2. Effects of trinexapac-ethyl (TE) and cytokinin on shoot density of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. BA, 6-benzyladenine; Ctrl, control.

treatment maintained a significantly higher leaf chlorophyll concentration at 4 to 8 d, TE maintained a significantly higher chlorophyll concentration at 4 to 16 d, and TE + BA maintained a significantly higher chlorophyll concentration during the entire period of heat stress. Compared with TE treatment, TE + BA showed a significantly higher chlorophyll concentration at 12, 16, and 20 d of heat stress.

Total nonstructural carbohydrate concentration. Leaf TNC concentration decreased with the progression of heat stress for all plants. The greatest decline in TNC concentrations occurred in control plants. All chemical-treated plants slowed the decline in TNC concentrations during heat stress compared with controls (Fig. 6). TE + BA-treated plants had the highest TNC concentration,

Fig. 3. Effects of trinexapac-ethyl (TE) and cytokinin on shoot growth rate of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. The line at the shoot growth rate of 8 mm every 4 d shows the initial level of shoot growth rate. BA, 6-benzyladenine; Ctrl, control.

Fig. 4. Effects of trinexapac-ethyl (TE) and cytokinin on clipping yield of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. The line at a clipping yield of $6.7 \text{ mg} \cdot \text{cm}^{-2} \cdot 4 \text{ d}$ shows the initial level of clipping yield. BA, 6-benzyladenine; Ctrl, control.

followed by TE- and BA-treated plants. Compared with the control, BA treatment maintained a significantly higher TNC concentration at 8, 12, and 20 d. TE + BA and TE treatments maintained a significantly higher TNC concentration during the entire period of heat stress.

Discussion

Previous work has shown that a decrease in cytokinin concentration could be related to turf quality decline in creeping bentgrass under heat stress conditions (Wang et al., 2003, 2004). Applying cytokinins or a cytokinin-containing seaweed extract has been found to improve leaf photosynthetic efficiency under heat stress conditions in creeping bentgrass (Liu and Huang, 2002), and has enhanced heat resistance of Kentucky blue-

Fig. 5. Effects of trinexapac-ethyl (TE) and cytokinin on leaf chlorophyll content of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. BA, 6-benzyladenine; Ctrl, control.

grass sod (Zhang et al., 2003) and drought resistance in creeping bentgrass (Zhang and Ervin, 2004). In this study, BA, a synthetic cytokinin, also showed the reduction of declines in turf quality at 8, 16, and 24 d of heat stress; shoot density at 12 d; shoot growth rate at 4, 8, and 16 d; clipping yield at 4, 12, 16, and 20 d; chlorophyll concentration at 4 and 8 d; and TNC concentration at 8, 12, and 20 d, confirming its positive effects to enhance heat resistance of creeping bentgrass. However, BA effects on heat resistance were relative minor when compared with TE and TE + BA.

Chlorophyll concentration decreased gradually with the progression of heat stress, which may contribute to decreases in photosynthetic rate (Grover et al., 1986; Harding et al., 1990). Plant respiration rate often increases under the heat stress (Huang and Gao, 2000; Ruter and Ingram, 1990, 1992), whereas photosynthetic rate decreases (Ziska, 1998). When plant respiration rate exceeds photosynthetic rate, this leads to increased carbon consumption (Huang and Gao, 2000), exhausting carbohydrate reserves in plant tissues. This imbalance in respiration to photosynthetic rate was noted with a decline in TNC concentrations during heat stress.

Shoot vertical growth rate is positively responsive to heat if within 5°C higher than the optimal temperature range in many plants (Criddle et al., 1997). In this study, shoot growth rate and clipping yield increased initially in response to heat stress. Such an initial increase may increase the energy demand and could accelerate excess carbon consumption unless carbon production is increased. However, as previously reported, carbon production through photosynthesis typically decreases while respiration increases with increasing temperatures (Criddle et al., 1997; Grover et al., 1986; Harding et al., 1990; Huang and Gao, 2000; Paulsen, 1994; Xu and Huang, 2001). Therefore, initial rapid increases in shoot vertical growth rate resulted in excess carbon loss by clipping removal and have negative effects on plant survival of long-term heat stress.

TE is a plant growth regulator that showed effects on reduced vertical growth (Beasley et al., 2005; Tegg and Lane, 2004), inhibiting turfgrass sod heating incited by sod respiration (Heckman et al., 2001), and increasing leaf cell density and chlorophyll concentration (Ervin and Koski, 2001), enhancing superoxide dismutase and photochemical activity (Zhang and Schmidt, 2000). Such suppressive effects could be beneficial to heat resistance of creeping bentgrass, because it may reduce clipping removal or respiratory energy consumption. In this study, TE reduced shoot growth rate before heat stress, which also sequentially suppressed excess shoot growth and clipping removal under the heat stress condition. Such effects on energy conservation was also indicated by the slower decline of leaf TNC concentration and steady shoot growth rate under the period of heat stress.

Fig. 6. Effects of trinexapac-ethyl (TE) and cytokinin on total nonstructural carbohydrate (TNC) in the leaves of creeping bentgrass under heat stress at a given day. Vertical bars at the top of the graph indicate LSD values ($P = 0.05$) for treatment comparisons on a given day after heat stress. Vertical bars on the right indicate LSD values ($P = 0.05$) for time course comparisons within a given treatment. The arrow indicates the time heat stress started. BA, 6-benzyladenine; Ctrl, control.

When compared with the TE treatment, TE + BA did not show a significant effects on clipping yield, shoot growth rate (except at 24 d), and turf quality (except at 20 and 24 d). The synergistic effects of TE and BA were more pronounced on chlorophyll concentration (at 12, 16, 20 d) and TNC concentration (at 8, 12, 20 d) when compared with TE-treated plants alone. TE is a growth retardant to reduce shoot vertical growth without negative rooting effects (McCullough et al., 2004). BA could enhance root cytokinin signaling to protect oxidative damages under heat stress (Wang et al., 2003). The synergistic effects of TE + BA on leaf chlorophyll concentration and TNC concentration could result from the combination of shoot growth reduction from TE and root growth regulation from BA. Ervin and Zhang (2003) reported that TE application can lead to an increase in leaf cytokinin levels in turfgrass. This may be a reason why there were no significant differences in turf quality, shoot growth rate, and clipping yield during the early stress period between TE + BA and TE treatment. Our results indicated that TE + BA or TE could be used to alleviate heat stress in creeping bentgrass.

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