

Timing and Temperature of Physiological Decline for Creeping Bentgrass

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ABSTRACT. Knowledge of the level of soil temperatures that is detrimental to shoot and root growth for cool-season grasses may help develop heat-tolerant plants and effective management practices to improve summer performance. The objectives of this study were to determine the level and duration of high temperatures in the root zone that will induce decline for various growth and physiological parameters and to compare the responses of different physiological parameters and cultivars to high root-zone temperatures. Nine creeping bentgrass [*Agrostis stolonifera* L. var. *palustris* (Huds.) Farw.] cultivars were subjected to eight root-zone temperatures (20, 21, 22, 23, 25, 27, 31, 35 °C) in water baths while exposed to a constant air temperature of 20 °C for 54 days. Root number, dry weight, and depth, active root biomass, turf quality, leaf cytokinin content, and canopy net photosynthetic rate (P_n), decreased in all nine cultivars as root-zone temperature increased from 20 to 35 °C, but the time and temperature at which the decline occurred varied for each parameter measured. P_n , cytokinin content, root number, and turf quality declined at 23, 27, 27, and 35 °C, respectively, after 28 days of exposure. Active root biomass, root number, root dry weight, turf quality, and rooting depth declined at 23, 25, 25, 25, and 35 °C, respectively, at 54 days. At a 31 °C root-zone temperature the decline in root number, cytokinin content, and turf quality occurred at 19, 37, and 47 days, respectively. The results suggest that root-zone temperatures of 23 °C or above this level were detrimental to root activities, P_n , and overall turf growth. Root and P_n decline at lower temperatures and earlier in the study than turf quality suggest that the disturbance of physiological activities of roots and leaves could lead to turfgrass quality decline at high root-zone temperatures.

Supraoptimal temperature is a major factor limiting shoot and root growth of cool-season plant species. Growth of creeping bentgrass, a widely used cool-season turfgrass on golf courses, often declines during extended periods of supraoptimal temperatures. The optimal temperature for the growth of cool-season grass is broadly ranged from 18 to 24 °C for shoot growth and 10 to 18 °C for root growth (Beard, 1973). Previous research has determined that high soil temperature was more detrimental than high air temperature in causing growth and physiological inhibition of shoots and roots in creeping bentgrass (Huang and Gao, 2000; Xu and Huang, 2000a, 2000b, 2001b) and other species (Kuroyanagi and Paulsen, 1988; Li et al., 1994; Todorovic et al., 1999). However, the critical level of supraoptimal root-zone temperatures and the duration of high-temperature stress causing physiological decline in creeping bentgrass have not been determined. Exact determination of injurious temperature levels could provide information for predicting timing and severity of physiological damages, which would help turfgrass managers to develop effective cultural practices to prevent decline of turfgrass stands during summer months.

Heat stress damage to plants involves changes of various physiological factors. The first visual signs of heat injury in turfgrasses include loss of turf color or leaf senescence and a decline in shoot density, which is often visually perceived as turf quality. Visual turf quality is the most widely used parameter to monitor turf performance in field and controlled environment studies (Bonos and Murphy, 1999; Jiang and Huang, 2000; Xu and Huang, 2000b, 2001a), although it may not provide the most information with respect to overall plant vigor. Photosynthesis is among the most sensitive physiological processes to increasing

temperatures (Crafts-Brandner and Salvucci, 2000b). Net photosynthetic rate (P_n) decreases as temperature increases above 30 °C in many cool-season plant species including turfgrasses (Al-Khatib and Paulsen, 1999; Crafts-Brandner and Salvucci, 2000b; Duff and Beard, 1974; Watschke et al., 1973; Xu and Huang, 2000a, 2000b, 2001a).

The production and viability of roots may play an important role in the adaptation of cool-season grasses to high soil temperatures. Root number, length, and mass are commonly used to evaluate root growth. Root viability, expressed as the percentage of live root tissues, has been used to monitor root activity under heat stress (Huang and Gao, 2000; Huang and Xu, 2000; Liu and Huang, 2000). Many researchers have reported that these root parameters decreased with increasing temperatures for various grass species in controlled environment experiments (Baret et al., 1992; Huang and Gao, 2000; Huang and Xu, 2000; Liu and Huang, 2000; Xu and Huang, 2000b, 2001a) and field studies (Beard and Daniel, 1966; Bonos and Murphy, 1999; Darrow, 1939; Howard and Watschke, 1991; Kuroyanagi and Paulsen, 1988; Ralston and Daniel, 1972). Cytokinins are produced mainly in roots, and may regulate shoot responses to high root-zone temperatures. Shoot growth inhibition and leaf senescence during heat stress has been associated with decreases in turfgrass cytokinin levels (Liu and Huang, 2002; Liu et al., 2002) and other plant species (Caers et al., 1985; Kuroyanagi and Paulsen, 1988; Udomprasert et al., 1995). The critical level of supraoptimal root-zone temperatures that causes detrimental effects may vary with plant parameters. However, the relative sensitivity of creeping bentgrass shoot and root parameters when subjected to high root-zone temperatures is not clear.

The objectives of this study were to 1) determine temperatures causing decline for various growth and physiological parameters of shoots and roots, 2) determine the duration of heat stress when the decline occurs for each parameter for nine creeping bentgrass cultivars, and 3) compare whether different shoot and root pa-

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rameters and cultivars vary in the level and/or duration of high root-zone temperatures.

Methods and Materials

PLANT MATERIAL AND GROWTH CONDITIONS. Nine creeping bentgrass cultivars were selected to represent older and newly developed cultivars ('Century', 'Crenshaw', 'L-93', 'Penn A-4', 'Penn G-6', 'Penncross', 'Putter', 'SR1020', 'Viper'). Grass sods (≈ 0.5 cm thick) of these cultivars were collected from turfgrass plots established for 2 years in the Hort Farm II at Rutgers Univ. in North Brunswick, N.J. Sodds were washed with water to completely remove the soil and then transplanted into clear polyethylene bags (5 cm in diameter and 40 cm in length, with eight holes drilled at the bottom for drainage), which were filled with washed sand (particle size of 0.2 to 0.5 mm) commonly used on golf greens. The polyethylene bags were placed in opaque polyvinylchloride (PVC) tubes of the same diameter and length, which were installed vertically in water baths with the lower open end exposed from the bottom of the water bath for drainage. The tubes were designed to enable plant growth to occur in well-drained sand in polyethylene tubes, while root-zone temperature was controlled at constant levels. A diagram of the water bath was presented in Wang et al. (2003).

Plants were grown in a growth chamber at 20 °C (day/night), a photosynthetic photon flux density of 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and a 14-h photoperiod for 60 d prior to the treatments. Before and during the experiment, the turf was mowed daily at 3 mm above the soil surface with scissors, watered daily to field capacity, and fertilized weekly with 50 mL of full-strength Hoagland's nutrient solution (Hoagland and Arnon, 1950).

Shoots were maintained at 20 °C in the growth chamber. Root-zone temperatures were controlled at a constant day/night level of: 20 (control), 21, 22, 23, 25, 27, 31, and 35 °C by keeping the entire root-zone (40-cm-long sand column in a polyethylene bag) in different sub-compartments in a water bath while the turf canopy was kept ≈ 1.0 cm above the water level in the water bath. The corresponding canopy temperatures were 20, 19, 19, 20, 20, 21, 22, and 23 °C. A gradient of root-zone temperatures was created in separate sub-compartments in a water bath. A heater was installed at one end of the water bath to heat water in this compartment to 38 °C. At the opposite end of the water bath, cool water (20 °C) was added to maintain root-zone temperature at 20 °C. Water levels were maintained at the top edge of the water bath, which was 0.5 cm below the top edge of PVC tubes. Root-zone temperatures were monitored weekly using thermocouples permanently placed into the root-zone at a depth of 10 cm.

Temperature and cultivar factors were arranged in a split-plot randomized design with temperature as the main plot and cultivar as the subplot. Each root-zone temperature treatment was replicated four times using four separate water baths in a single walk-in growth chamber.

MEASUREMENTS. Turfgrass quality was visually rated on a weekly basis using a 1 to 9 scale (1 = dead, brown turf; 9 = green, dense, healthy turf). Plants rated 6 or greater were considered acceptable quality. The number of roots visible on the surface of the clear polyethylene bag was counted weekly in a 3 \times 3 cm window at 5 to 8 cm from the soil surface. At 28 d of treatment canopy net photosynthesis rate (P_n) of all nine cultivars was measured individually using a portable gas exchange system (LI-6400; LI-COR, Lincoln, Nebr.) with an auxiliary chamber for canopy measurement.

Leaf cytokinin content was measured in 'Penn A-4' and 'Putter' using the procedure described in Setter et al. (2001). Leaf tissue was harvested weekly and flash frozen in liquid nitrogen. Cytokinins were extracted in 80% (v/v) methanol. Extracted cytokinins were bound to C18-silica columns (SPE-96; Supelco, Bellefonte, Pa.) and eluted with a tri-ethylamine-acetate/methanol solution. Radiolabeled cytokinins (Amersham Co., Arlington Heights, Ill.) were added to monitor purification efficiency, which never fell below 90% efficiency. An indirect enzyme-linked immunosorbent assay (ELISA) was used to quantify three kinds of cytokinins, trans-zeatin/zeatin riboside, dihydrozeatin/dihydrozeatin riboside, and isopentenyl adenosine. The three measured cytokinins were added together for total cytokinin content. Samples from the silica columns were dried in vacuum at room temperature and dissolved in Tris buffer. ELISA plates were coated overnight at 4 °C with corresponding cytokinin-bovine serum albumin conjugate in carbonate buffer. Plates were washed and a monoclonal antibody for each cytokinin was added in Tris buffer, and incubated overnight at 4 °C. Secondary antibody, anti-mouse IgG-alkaline phosphatase conjugate, was added in Tris buffer and incubated overnight at 4 °C. Plates were washed and developed with p-nitrophenyl phosphate solution for 1 h at room temperature. A_{405} was measured with a plate reader (model EL 800; Bio-Tek Instruments, Winooski, Vt.) and samples were quantified using known standards.

At 54 d of treatment, plants were harvested, roots were washed clean of sand, and roots were excised from shoots. Maximum rooting depth was measured with a ruler. Roots were then dried in an oven at 80 °C for 3 d and root dry weight (RDW) was determined. Approximately 1.5 g of fresh roots from 'Putter', 'Penncross', and 'Penn A-4' were used for root viability measurements as modified from Knievel (1973). Roots were incubated in the dark for 24 h in 0.6% 2,3,5-triphenyltetrazolium chloride at 30 °C. Roots were rinsed with deionized water and placed in 95% ethanol at 70 °C for formazan extraction. Final volumes were adjusted and A_{490} was measured with a spectrophotometer (Spectronic Instruments, Rochester, N.Y.). Live roots were mixed with different proportions of autoclave-killed roots to construct a standard curve. Root viability was expressed as viable root biomass, or dry weight of viable roots per tube (91.4 cm^3).

Effects of root-zone temperature, cultivar, duration of treatment, and their interactions were determined by the analysis of variance according to the general linear model procedure of the Statistical Analysis System (SAS Institute, Cary, N.C.). Differences among treatments, cultivars, and durations of treatments were determined by the least significance difference (LSD) test at the 0.05 probability level.

Results

TIME, TEMPERATURE, AND CULTIVAR INTERACTIONS. Main effect responses for time, temperature, and cultivar were significant ($P \leq 0.05$) for all measured parameters, except time for parameters that were only measured once. All one-way interactions were significant except for cultivar \times temperature for P_n , root dry weight, and viable root biomass. Three-way interactions were not significant for any measured parameter.

TURFGRASS QUALITY. Turfgrass quality at 20 °C root-zone temperature did not change for any cultivar during the entire treatment period (Fig. 1A). At 25 °C (Fig. 1B), 31 °C (Fig. 1C), and 35 °C (Fig. 1D), turfgrass quality of all nine cultivars began to decline at 47, 40, and 33 d, respectively. No cultivar differences were

observed at 20 °C (Fig. 1A) ‘Putter’, however, consistently had the lowest quality after extended periods of treatment at 25–35 °C (Figs. 1B, 1C, 1D). Other cultivars did not show consistent differences in turf quality at different temperatures (Fig. 1A–D).

Turf quality of all nine cultivars remained constant for the first 19 d of exposure to all root-zone temperatures (Fig. 2 A and B). At 40 and 54 d, turf quality decline occurred at 31 °C (Fig. 2C) and 25 °C (Fig. 2D), respectively.

ROOT CHARACTERISTICS. Root number at 5–8 cm in all cultivars increased over time at 20 °C (Fig. 3A). At 25, 31, and 35 °C, root number decreased at 47, 19, and 12 d of treatment, respectively (Fig. 3 B and D). ‘Penn A-4’ had the greatest number of roots among all nine cultivars at 20 °C (Fig. 3A) and 31 °C (Fig. 3C). There was no consistent cultivar variation in root number at 25 and 35 °C (Fig. 3 B and D).

There was no consistent change in root number with temperature at 4 d of treatment for any cultivar (Fig. 4A). After 19, 40, and 54 d, root number decreased at 27, 25, and 23 °C, respectively, for all cultivars (Fig. 4B–D).

Maximum rooting depth became shallower as temperature increased from 20 to 35 °C for all cultivars (Fig. 5A). ‘Penncross’ had the longest rooting depth at 20–23 °C, but the shortest rooting depth at 35 °C among all nine cultivars. There were no consistent differences in rooting depth among other cultivars at different root-zone temperatures. Decline in root dry weight was observed when soil temperature was increased to 27 °C or higher levels (Fig. 5B). At 35 °C, ‘Penncross’ and ‘Penn G-6’ had the lowest root dry weight and ‘Penn A-4’ had the greatest.

Root viability also decreased as root-zone temperatures increased from 20 to 23 °C or higher (Fig. 6). ‘Penncross’ had the lowest root viability among the three cultivars at root zone temperatures from 21 to 35 °C.

TEMPERATURE RESPONSE OF PHYSIOLOGICAL FACTORS. The differences in the sensitivity of leaf P_n (A), leaf cytokinin content (B), root number (C), and turf quality (D) to increasing root-zone temperatures at 26 to 30 d of treatment were compared in Fig. 7. P_n for all cultivars began to decrease at root-zone temperatures as low as 23 °C at 28 d of treatment (Fig. 7A). P_n averaged over cultivars at 35 °C was <50% of that at 20 °C. Total cytokinin content in leaves began to decrease at 31 and 27 °C following 30 d of treatment for ‘Penn A-4’ and ‘Putter’, respectively (Fig. 7B). Total cytokinin level at 35 °C was 75% of that at 20 °C. Root number decreased at 27 °C after 26 d of treatment for all cultivars (Fig. 7C). As temperature increased to 35 °C, root number was reduced to <30% of the level at 20 °C. Significant decline in turf quality did not occur until temperature increased to 35 °C at 25 d (Fig. 7D).

At 31 °C, turfgrass quality declined at 47 d of treatment (Fig. 8A), leaf cytokinin content at 37 d (Fig. 8B), and root number at 19 d (Fig. 8C). At the time of decline, turf quality and root number dropped to ≈50% of the initial value.

Discussion

Previous research broadly defined the optimum temperature for cool-season grasses in the range of 18 to 24 °C for shoot growth

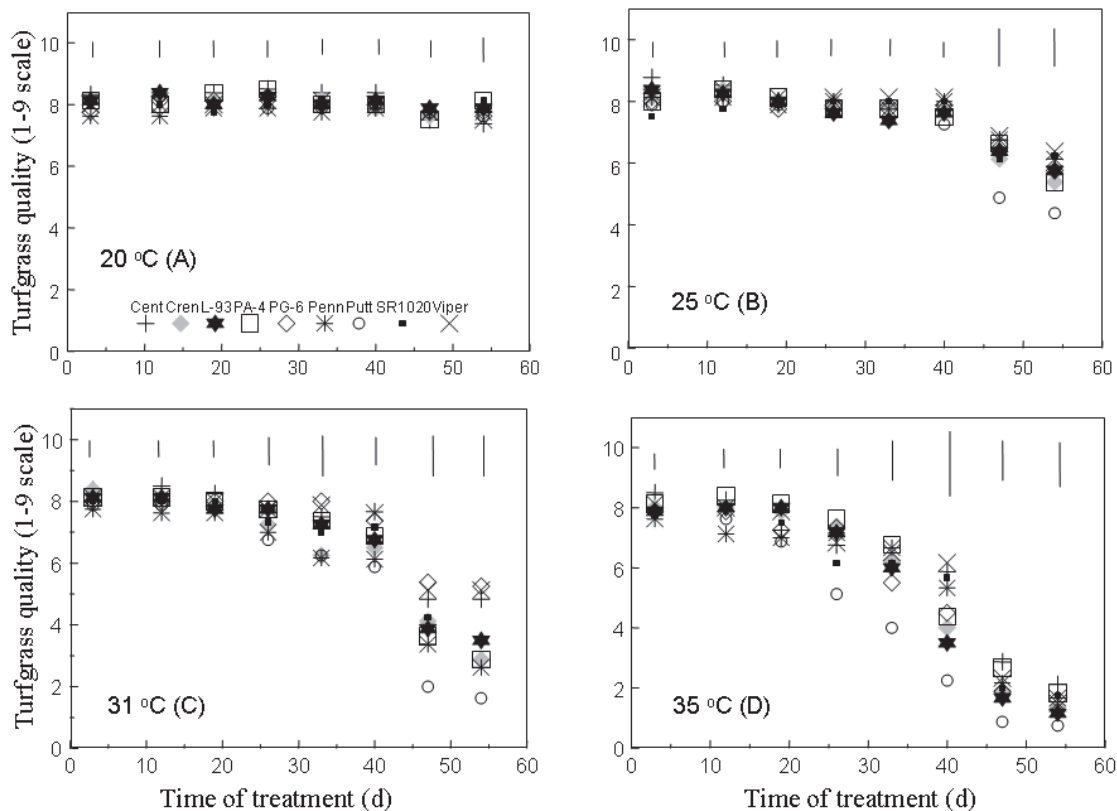


Fig. 1. Turfgrass quality changes over time for nine cultivars of creeping bentgrass at soil temperature of 20 °C (A), 25 °C (B), 31 °C (C), and 35 °C (D). Air temperature was held constant throughout the experiment at 20 °C for all treatments. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), L-93, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), SR1020, and ‘Viper’. Turfgrass quality was rated based on 1–9 scale, with 9 being the best. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given time of treatment. The LSD value for comparison over time of treatment was 0.6 at 20 °C (A), 0.4 at 25 °C (B), 0.5 at 31 °C (C), and 0.6 at 35 °C (D).

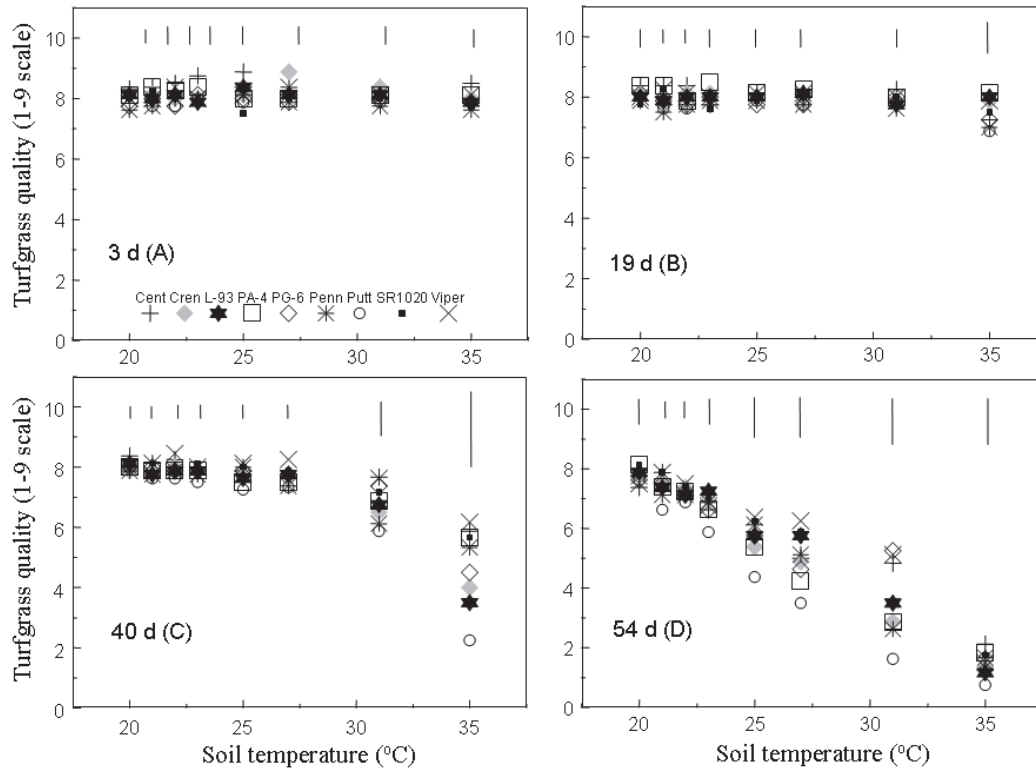


Fig. 2. Turfgrass quality changes with increasing soil temperatures for nine cultivars of creeping bentgrass at 3 d (A), 19 d (B), 40 d (C), and 54 d (D) of treatment. Air temperature was held constant throughout the experiment at 20 °C for all treatments. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), ‘SR1020’, and ‘Viper’. Turfgrass quality was rated based on 1–9 scale, with 9 being the best. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given soil temperature treatment. The LSD value for comparison among different temperatures was 0.3 at 3 d (A), 0.4 at 19 d (B), 0.5 at 40 d (C), and 0.5 at 54 d (D).

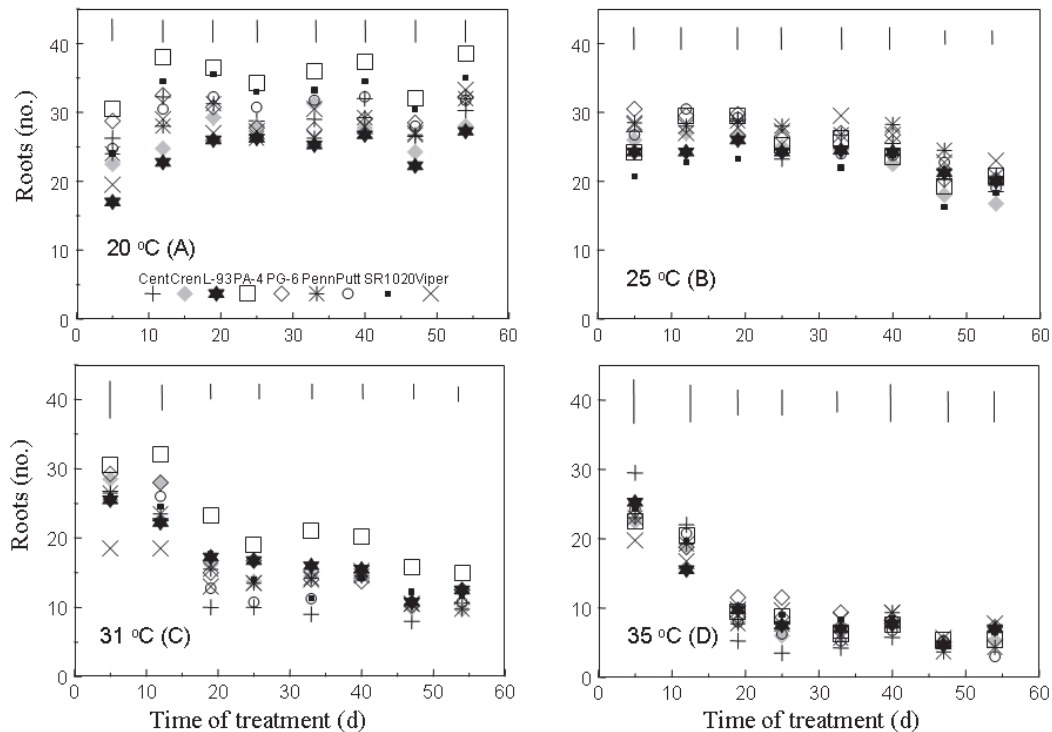


Fig. 3. Root number changes at 5–8 cm over time for nine cultivars of creeping bentgrass at soil temperature of 20 °C (A), 25 °C (B), 31 °C (C), and 35 °C (D). Air temperature was held constant throughout the experiment at 20 °C for all treatments. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), ‘SR1020’, and ‘Viper’. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given time and comparison of all times. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given time of treatment. The LSD value for comparison over time of treatment was 3 at 20 °C (A), 5 at 25 °C (B), 4 at 31 °C (C), and 4 at 35 °C (D).

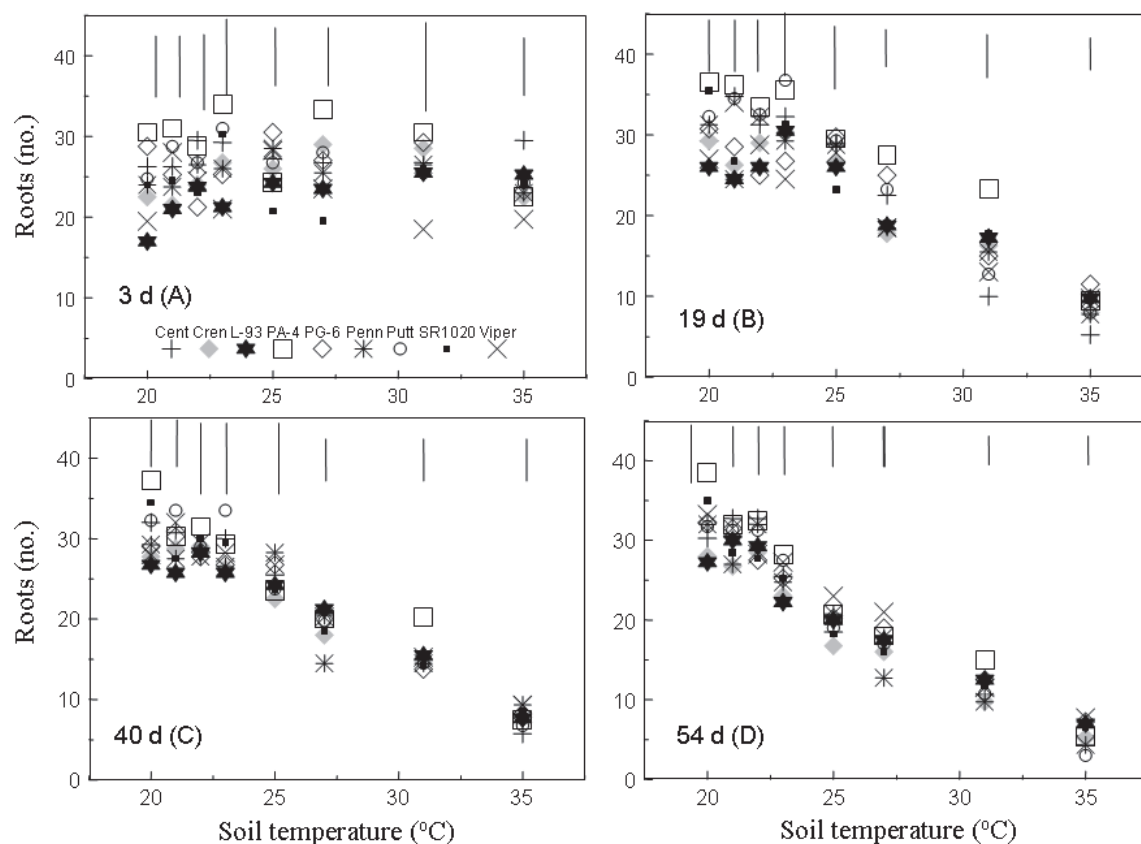


Fig. 4. Root number changes at 5–8 cm with increasing soil temperatures for nine cultivars of creeping bentgrass at 3 (A), 19 (B), 40 (C), and 54 (D) d. Air temperature was held constant throughout the experiment at 20 °C for all treatments. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), SR1020, and ‘Viper’. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given soil temperature treatment. The LSD value for comparison among different temperatures was 3 at 3 d (A), 2 at 19 d (B), 2 at 40 d, and 2 at 54 d (D).

and 10 to 18 °C for root growth, without differentiation between air and soil temperatures, growth and physiological parameters, and grass species or cultivars (Beard, 1973). The present study found that when roots only were exposed to root-zone temperatures of 20–22 °C while air temperature was at 20 °C, turf quality of all nine creeping bentgrass cultivars was maintained at a high level and root number increased during the entire treatment period (54 d), indicating that root-zone temperatures of 20–22 °C is not detrimental to either root or shoot growth of creeping bentgrass. The critical level of elevated root-zone temperatures that was detrimental for creeping bentgrass changed with treatment duration and varied with growth and physiological parameters, but did not differ among cultivars.

The level of root-zone temperatures that caused heat injuries was reduced with longer exposure duration of plants to high temperatures for all cultivars. Turf quality did not decline when root-zone temperatures increased from 20 to 35 °C within the first 19 d of treatment whereas the decline in turfgrass quality occurred at 25–27 °C, depending on cultivar, by the end of the treatment period (54 d) (Fig. 1). Huang and Gao (2000) reported the decline in turf quality of three creeping bentgrass cultivars occurred when both air and soil temperatures increased to 30 °C for 20 d. Root number declined at 27 °C at 19 d of treatment. As the exposure duration prolonged to 54 d, root number and viable root biomass decreased at root-zone temperatures as low as 23 °C. The declines in root dry weight and maximum rooting depth were observed at higher temperatures than root number and viable root biomass, particularly rooting depth (35 °C). The lower

temperature of decline for root number and viable root biomass suggests that these two parameters were more sensitive to high root-zone temperatures than root dry weight and rooting depth. This illustrates the importance of maintaining viable roots in order for plants to survive high soil temperatures.

The exposure duration to high root-zone temperature that caused physiological decline varied with plant parameters. For example, when soil temperature was raised to 31 °C, root number declined at 12 d, cytokinin content at 30 d, and turf quality at 40 d of treatment (Fig. 7). Previous research also reported earlier decline in root number than turf quality in creeping bentgrass when exposed to a high soil temperature (35 °C) (Xu and Huang, 2000b, 2001a). Root characteristics declined earlier than shoot characteristics in other species during heat stress (Aloni et al., 1992; Du and Tachinbana, 1994; Kuroyanagi and Paulsen, 1985, 1988). Our results confirmed that root deterioration well preceded turf quality decline at high root-zone temperatures.

The comparison of responses of P_n , leaf cytokinin content, turf quality and root number to increasing root-zone temperature indicates that P_n was most sensitive to elevated root-zone temperatures (Fig. 8). P_n dropped significantly at 23 °C following 28 d of treatment. Within the same time period, significant decline did not occur until 27–31 °C for leaf cytokinin content (varied with cultivars), 27 °C for root production, and 35 °C for turf quality. The rapid reduction in photosynthetic rate in response to elevated soil temperatures could be due to stomatal closure (Graves et al., 1989; Gur et al., 1976; Martin et al., 1989) and decreased enzyme activity, such as Rubisco (Bose et al., 1999; Xu

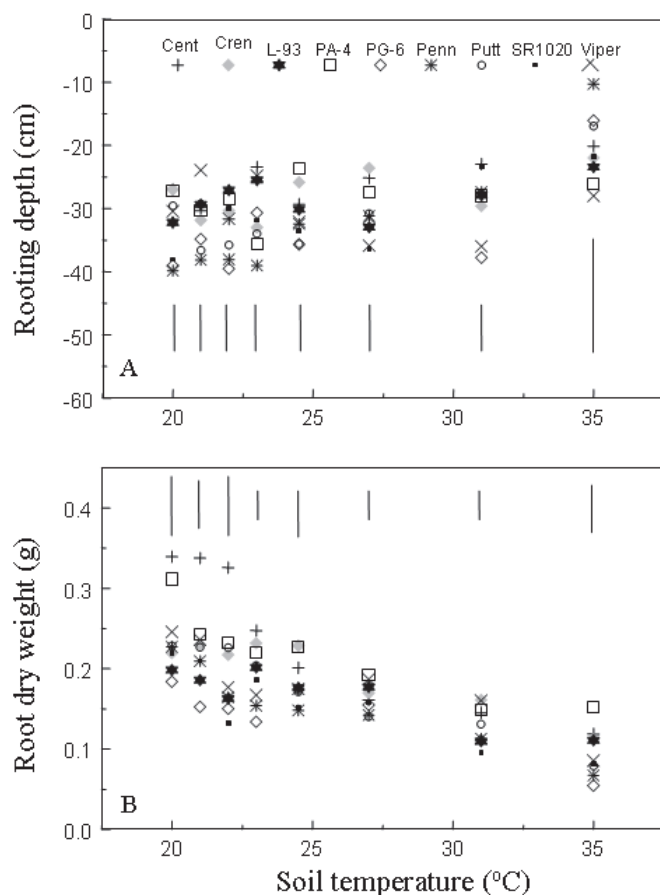


Fig. 5. Rooting depth (A) and root dry weight (B) changes with increasing soil temperatures for nine cultivars of creeping bentgrass after 54 d. Air temperature was held constant throughout the experiment at 20 °C for all treatments. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), ‘SR1020’, and ‘Viper’. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given soil temperature treatment. The LSD value for comparison among different temperatures was 8 for rooting depth (A) and 0.22 for root dry weight (B).

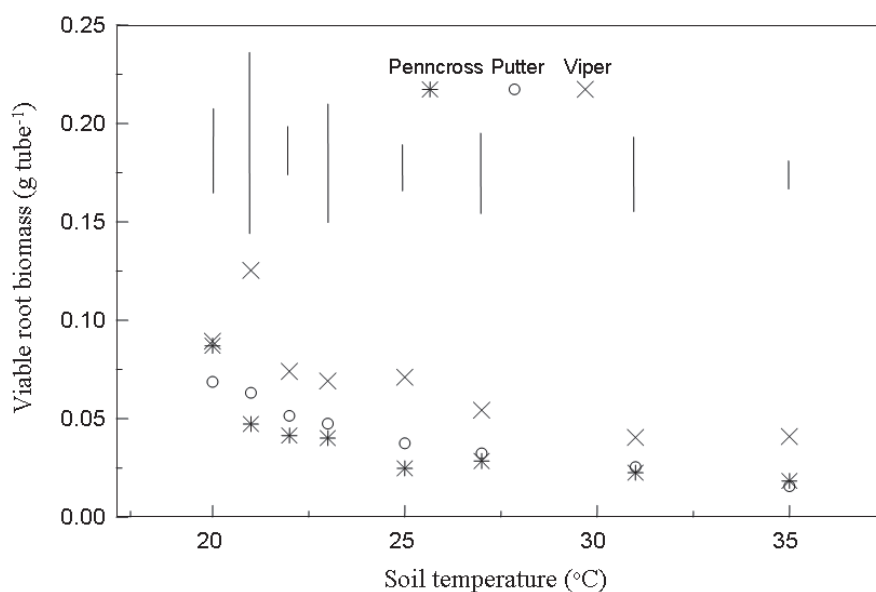


Fig. 6. Viable root biomass changes with increasing soil temperatures for three creeping bentgrass cultivars (‘Penncross’, ‘Putter’, and ‘Viper’) after 54 d. Air temperature was held constant throughout the experiment at 20 °C for all treatments. Vertical bars indicate LSD values ($P \leq 0.05$) for cultivar comparisons at a given soil temperature treatment. The LSD value for comparison among different temperatures was 0.023.

and Huang, 2001a), Rubisco activase (Law and Crafts-Brandner, 1999; Salvucci et al., 2001; Sharkey et al., 2001; Weis, 1981), and the oxygen-evolving complex (Al-Khatib and Paulsen, 1999; Downs et al., 1999; Heckathorn et al., 1999). Decreased P_n results in decreased availability of carbohydrate, which may lead to decreased carbon allocation to roots (Todorovic et al., 1999; Udomprasert et al., 1995; Xu and Huang, 2000a; Xu et al., 2000). As root production decreased, cytokinin production in roots would decrease and this in turn limits cytokinin supply to shoots, causing leaf senescence (Kuroyanagi and Paulsen, 1988) and turf quality decline (Liu et al., 2002). Turf visual quality has been a most widely used parameter in the evaluation of turf performance. Our results suggest that physiological changes under heat stress would provide earlier signs of heat injury than visual rating of turf quality.

Cultivar variations in physiological responses were expressed mainly at higher root-zone temperatures (31 and 35 °C), suggesting that selection of plant materials for heat tolerance should be performed at these or higher root-zone temperatures. However, there was generally lack of consistent variation in physiological responses to high root-zone temperatures among the nine cultivars examined, with few exceptions: at 31 or 35 °C, ‘Putter’ had lowest turf quality (Fig. 1 C and D); ‘Penn A-4’ had most roots (Fig. 1C); ‘Penncross’ had the shallowest rooting depth (Fig. 5A).

In summary, the growth and physiological activities of both roots and shoots declined when plants were exposed to elevated root-zone temperatures above 23 °C for extended periods of time (54 d). The root-zone temperature that caused the decline varied with plant parameter and stress duration, but was not affected by cultivar. The decline in P_n , root production and activities occurred at lower root-zone temperatures and earlier during the treatment compared to turf quality. Therefore, effective management practices, such as syringing and inserting fans, should be taken when physiological signs of heat injury occur and when soil temperature reaches the minimum detrimental levels to prevent declines in visual turf quality during summer months. These data also indicate that turfgrass quality may not be the best parameter to use for assessing heat tolerance in breeding programs.

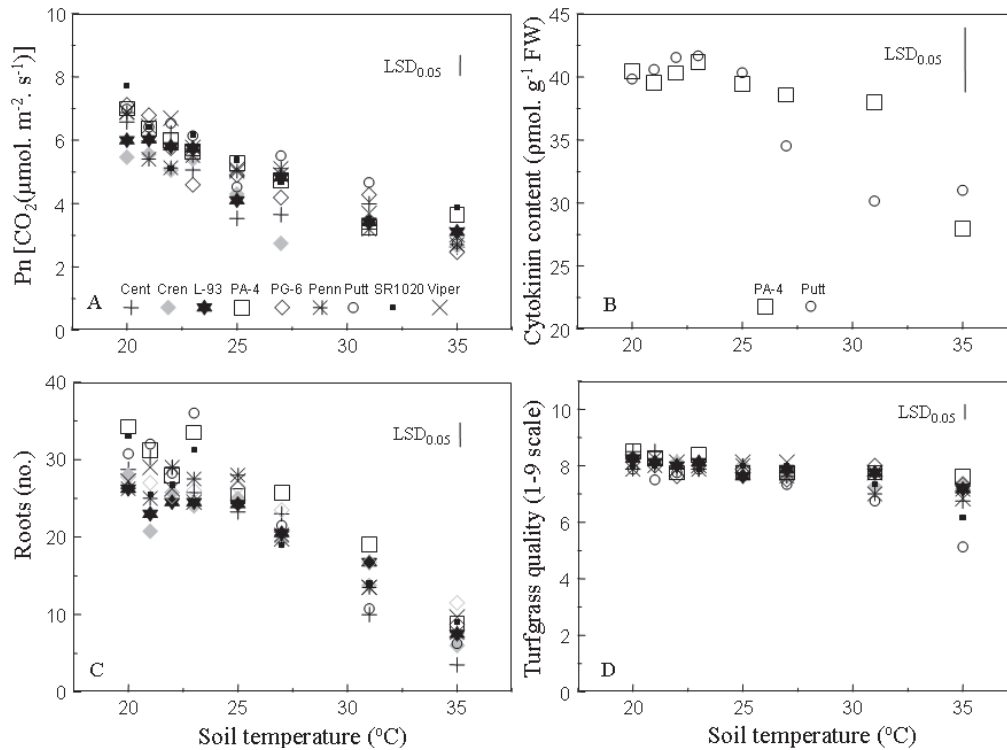


Fig. 7. Changes in canopy net photosynthetic rate (P_n) (A), leaf cytokinin content (B), root number (C), and turfgrass quality (D) for different creeping bentgrass cultivars with increasing soil temperatures. The four parameters were measured between 26–30 d of treatment. Data were from nine cultivars for P_n , root number and turf quality and two cultivars for cytokinin content. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), ‘SR1020’, and ‘Viper’. Air temperature was held constant throughout the experiment at 20 °C for all treatments. The LSD value ($P \leq 0.05$) for comparison over time of treatment was 0.6 for P_n (A), 5.1 for cytokinin content (B), 3 for root number (C), and 0.6 for turf quality (D).

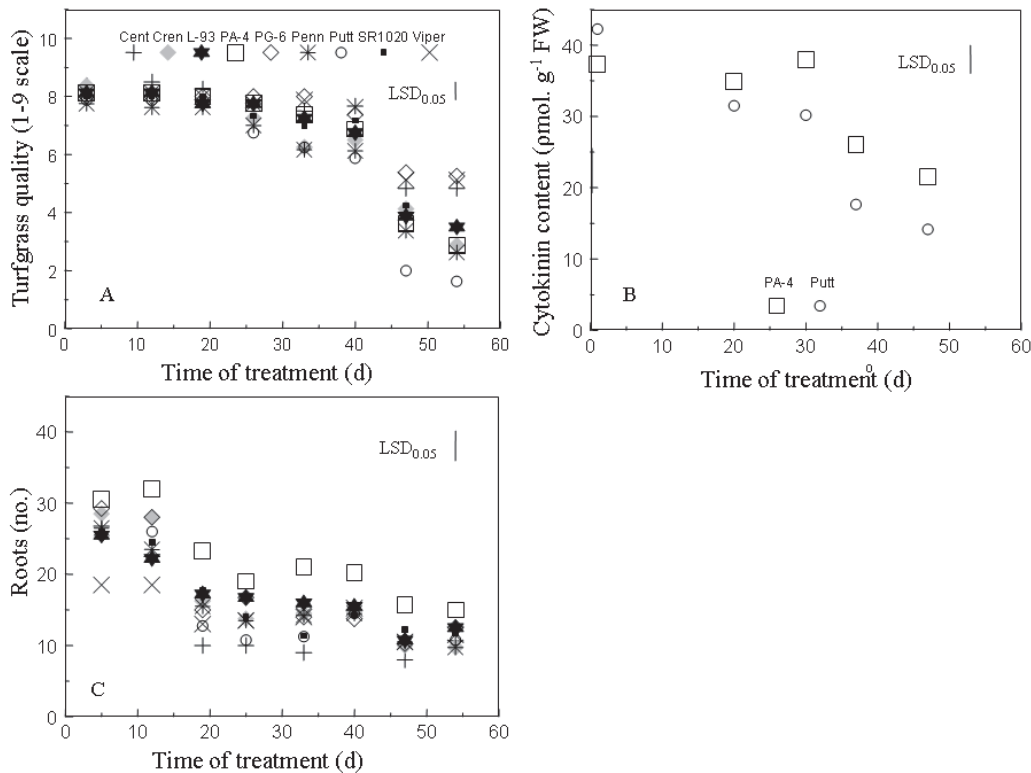


Fig. 8. Changes in turf quality (A), leaf cytokinin content (B), and root number (C) over time at 31 °C for different creeping bentgrass cultivars. Data were from nine cultivars for root number and turf quality and two cultivars for cytokinin content. Cultivars were ‘Century’ (Cent), ‘Crenshaw’ (Cren), ‘L-93’, ‘Penn A-4’ (PA-4), ‘Penn G-6’ (PG-6), ‘Penncross’ (Penn), ‘Putter’ (Putt), ‘SR1020’, and ‘Viper’. Air temperature was held constant throughout the experiment at 20 °C for all treatments. Turfgrass quality was rated based on 1–9 scale, with 9 being the best. The LSD value ($P \leq 0.05$) for comparison over time of treatment was 0.4 for turf quality (A), 4.2 for cytokinin content (B), and 4 for root number (C).

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