Soil CO₂ Concentration Effects on Creeping Bentgrass Grown under Various Soil Moisture and Temperature Conditions

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Abstract. Use of creeping bentgrass [*Agrostis stoloniferous* L. var. *palustris* (Huds.)] on golf greens has expanded into the hotter, more humid regions of the United States where its quality is often low during summer months. The summer decline in bentgrass quality may be partially attributed to respiration rates exceeding photosynthesis during periods of supraoptimal temperatures and adverse soil conditions, such as excessive CO₂ and inadequate O₂ levels. The objectives of this study were to examine the effects of high temperature, high soil CO₂, and irrigation scheduling on creeping bentgrass growth. A growth chamber study was conducted using 'A-1' creeping bentgrass. Treatments included all combinations of three day/night temperature regimes (26.5/21 °C, 29.5/24 °C, and 32/26.5 °C), three irrigation schedules (field capacity daily, field capacity every two d, and half field capacity daily), and four soil CO₂ injection levels (10%, 5%, 0.03%, and a noinjection control). Creeping bentgrass shoot and root dry weights and net photosynthetic rates were greater for day/night temperatures <32/26.5 °C. High temperatures (32/26.5 °C) and 10% CO₂ reduced bentgrass net photosynthesis by 37.5 µmol CO₂/m²/s. Shoot and root total nonstructural carbohydrates also were lowest for highest temperature regime. Respiration exceeded gross photosynthesis at 32/26.5 °C when 5% and 10% CO₂ injection levels were used, indicating a carbon deficit occurred for these conditions. Irrigation volume and frequency did not affect bentgrass growth. High temperatures combined with high soil CO₂ levels produced poorest turf quality.

Creeping bentgrass [*Agrostis stoloniferous* L. var. *palustris* (Huds.)] is the cool-season grass most widely used on golf greens (Beard, 1982). Preference for the superior putting surface of bentgrass has led to its use in the hotter, more humid regions of the United States where its quality often declines during summer months. This condition is referred to as summer bentgrass decline (McCarty, 2005).

Factors contributing to summer decline of bentgrass include poor soil aeration, excessive or deficient soil water, high relative humidity, high temperatures, and soil-borne disease organisms. Supraoptimal temperatures cause root loss, reduced shoot and tiller growth, and reduced shoot density in creeping bentgrass (Dipaola and Beard, 1992; Huang et al., 1998a, 1998b; Krans and Johnson, 1974). This growth decline is attributed to a reduction in photosynthesis and an increase in respiration at temperatures above 30 °C (Huang

et al., 1998a; Huang and Gao, 2000). Imbalance between photosynthesis and respiration leads to a reduction in carbohydrate accumulation (Huang et al., 1998a; Huang and Gao, 2000) and lower carbohydrate availability may be responsible for reduction of growth (Baker and Jung, 1968; Dipaola and Beard, 1992; Liu and Huang, 2000; Watschke et al., 1970, 1972).

The composition of the soil atmosphere may also affect bentgrass survival. During hot summer months, soil O₂ levels can become depleted due to increased root and microbial respiration (Waddington and Baker, 1964; Williamson, 1964). Creeping bentgrass root viability and dry matter are reduced under high air (35 °C) and soil (25 °C) temperatures and limited soil O₂ concentration (2.0 × 10⁻⁷ g·cm⁻²·min⁻¹) (Huang et al., 1998a). Saturated or anoxic soil conditions limit bentgrass root length (Huang, 1997). Although some plants are able to develop a dense, shallow root system to take advantage of more favorable O₂ conditions (Glinski and Stepniowski, 1985), roots of most crop plants are unable to survive at O₂ levels <2% to 5% with optimum levels between 5% and 15% (Barden et al., 1987). Minimum O₂ levels for

maintaining creeping bentgrass quality have not been established.

Due to root and microbial respiration, soil CO₂ can reach levels often to one hundred times greater than in atmospheric air (Bremner and Blackmer, 1982; Hillel, 1980). Elevated CO₂ levels may adversely affect roots by decreasing root cytoplasmic pH and interfering with water and nutrient uptake (Chang and Loomis, 1945). Soil CO₂ levels ≥2.5% reduced creeping bentgrass root dry weight by 40% and root length by 2 to 3 cm when grown under greenhouse conditions (Bunnell et al., 2002).

Although golf greens grown on sand mixes have lower CO₂ levels than unamended soils (Kavanagh and Jelley, 1980), thatch, surface compaction, algae, and a dense turf may decrease gas diffusion. Golf greens are typically watered frequently during summer months due to high evapotranspiration rates. Jordan (1998) reported irrigation of bentgrass greens increased soil CO₂ concentrations from 0.8% to 2.8% and attributed the increase to limited gas exchange due to soil water.

Forcing air into or out of a U.S. Golf Association (USGA) green rootzone (USGA Green Section Staff, 1960) through subsurface drain lines may improve soil conditions for bentgrass growth. Preliminary studies by Dodd et al. (1999) indicate increased soil O₂ and decreased CO₂ levels with both pressure and vacuum induced subsurface air movement treatments in a USGA bentgrass green. No root or shoot growth differences were observed. Similar experiments using vacuum or pressure modes conducted on USGA bentgrass greens have reported 50% to 80% reductions in soil CO₂ (Bunnell et al., 2004) or soil gases remaining close to atmospheric levels (Bigelow et al., 2001). These studies reported little effect on bentgrass growth or rooting, however.

The objective of this study was to examine the effects of high soil CO₂ concentrations on creeping bentgrass grown under various soil moisture and temperature conditions.

Materials and Methods

A growth chamber study was conducted in 2001 and 2002 to examine whether temperature and soil moisture influence the tolerance of bentgrass to various soil CO₂ levels. Growth cells were constructed to simulate a USGA green in growth chambers. Plexiglass tubes 30 cm tall with a 5-cm diameter were used as growth cells. Cell bottoms were sealed with fabricated plastic caps and epoxy. Each cap was fitted with air-tight, quick-disconnect fittings for attaching 0.95-cm-diameter tubing. The bottom of each cell was filled with 6–12 mm diameter gravel to a depth of 5 cm. Fifteen cm of USGA specified 85 sand : 15 peat soil mix was placed on top of the gravel. Plugs of 'A-1' creeping bentgrass (10 cm height × 5 cm diameter) were harvested from an experimental USGA green in Clemson, S.C., and placed on top of the soil mix in each cell. Newly planted growth cells were saturated with water and allowed to drain freely for 24 h. After draining, the outer walls of each cell were wrapped in aluminum foil to prevent light entry into the root zone, and the weight of each cell

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at field capacity was determined.

Completed growth cells were then placed in growth chambers and allowed to acclimate to the light and temperature regime of the chamber for a period of 14 d before soil gas injections were initiated. During this 14 d acclimation, foliage was maintained at a height of 4 mm. Cells were watered every other day during this period by weighing each cell and applying enough water to bring the growth cell back to field capacity. Cells were fertilized using a 10–10–10 solution at an N rate of 12 kg-ha⁻¹ beginning the day before treatments were initiated and continuing once every 14 d.

PVC lines 3 cm in diameter were used for removing water that drained from the cells and for supplying soil gases to the cells. The PVC lines were constructed with 30-cm deep p-traps that allowed water to drain from the cells but did not allow air to escape or enter, and the lines were connected to solenoid valves that regulated the timing and duration of gas injections from pressurized tanks. Latex balloons were fitted over the open end of each p-trap to provide additional pressure and prevent drained water from blowing out. Soil gases were injected into the cells through 0.95-cm diameter tubes attached to the PVC lines. Based on preliminary studies, it was determined that soil gases could be maintained in the cells at assigned levels by injecting gas mixtures once every 20 min for a duration of 1 min.

The 3 × 3 × 4 factorial experiment provided three replications per treatment combination and was conducted in a completely randomized split-plot design. Treatments included all combinations of three temperature regimes, three irrigation schedules, and four soil gas injection levels. The temperature regimes were randomly assigned to the growth chambers (whole plots) that contained growth cells for all combinations of the two sub-plot factors, irrigation and soil gases. Temperature regimes consisted of the day/night temperatures 26.5/21 °C, 29.5/24 °C, and 32/26.5 °C to simulate typical summer climates in the southern region of the U.S. Irrigation regimes consisted of weighing each cell and adding appropriate amounts of water to either

bring the cell to field capacity daily, every 2 d, or one-half field capacity daily. The four soil gas injection levels are described in Table 1.

Cells were subjected to the treatments for 6 weeks. Light intensity was 550 μmol-m⁻²·s⁻¹ at the turf surface. Turf was mowed every 2 d at a height of 4 mm throughout the experiment. Data was collected on net photosynthesis and dark respiration, shoot and root dry weights, and shoot and root total nonstructural carbohydrate (TNC) concentrations.

Net photosynthesis and dark respiration were measured after 6 weeks of treatment using an open gas exchange system as described in Miller et al. (1996). Cell drainage and gas-injection openings were plugged during sampling. A gas exchange chamber was constructed to fit directly on top of a growth cell. A clear plexiglass growth cell tube was cut to a height of 15 cm. The top was covered with a clear disposable petri dish and sealed with clear silicone adhesive. The chamber was sealed atop each cell during measurements using a clear plastic end cap with the bottom removed. A 0.6-cm-diameter inlet was drilled at a height of 1.5 cm above the open end of the chamber. An aquarium-type electric air pump with a 0.6-cm-diameter tube was used to provide positive air flow to the chamber inlet at 0.0183 L·s⁻¹. One 0.03-cm-diameter outlet was drilled 1 cm from the top of the chamber for a gas sampling tube. Laminar flow from inlet to outlet was prevented by using a piece of tape as a deflector at the inlet. Chamber air samples were taken by inserting 2 cm of a 0.02-cm-diameter air sampling tube through the chamber outlet. Change in CO₂ concentration was measured using a portable, infrared gas analyzer (CIRAS-1; PP Systems, Haverhill, Mass.) after 2 min to allow the chamber to reach equilibrium. Net photosynthesis measurements were taken between 1200 and 1400 HR and dark respiration measurements were taken between 0000 and 0200 HR.

Upon completion of the experiment, plant carbohydrates were analyzed (Westhafer et al., 1982) by initially dismantling each experimental cell to partition plant biomass into shoots and roots. Shoots and roots were washed free of soil, flash-frozen by immersing in liquid N₂, and freeze-dried for 6 d. Root and shoot dry weights were recorded, and samples were prepared for carbohydrate analysis by grinding in a cyclone mill (Udy Sample Mill; Udy Corp., Fort Collins, Colo.) to pass through a 1-mm screen. Shoot and root tissue carbohydrates were extracted following grinding. Shoot or root tissue (50 mg) was placed into glass test

tubes and rehydrated by adding 100 μL of 80% ethanol. Two mL of 0.1 M sodium acetate buffer (pH 4.5) was pipetted into each tube, vortexed, stoppered, and incubated for 1 h in a 100 °C water bath. Following removal, samples were vortexed, allowed to cool for 1 h, and placed back into the 100 °C bath for 1 h after which samples were cooled to 20 °C. Invertase (1 mL) (Sigma, I-4504, 5 units/mL in 0.1 M acetate buffer at pH 4.5) was added to each tube to break sucrose down into glucose followed by 1 mL of Rhizital amyloglucosidase preparation (A-7255; Sigma, 50 units/mL in 0.1 M acetate buffer). Samples were vortexed, stoppered, and incubated at 40 °C for 48 h in a water bath with periodic vortexing and then stored at 3 °C. Enzyme blanks were included.

Samples were analyzed for TNC using a modification of Nelson's Assay (Nelson, 1944; Somogyi, 1945). Standards of 0.0 to 0.7 μmol glucose/100 μL H₂O were used to prepare a standard curve for use with the shoot and root carbohydrate extracts. Aliquots (25 μL) of the root and shoot sample extracts were pipetted into test tubes. After 1 mL of copper reagent was added to each tube, samples were gently shaken and heated in a 100 °C water bath for 20 min. Samples were removed, lightly shaken, and allowed to cool in a room-temperature water bath for 5 min. Samples were again shaken before adding 0.5 mL of arsenomolybdate reagent and mixing. Absorbance measurements were taken at 520 nm zeroed on a 0.0 μmol/100 μL glucose standard using a Beckman DU-64 spectrophotometer (Beckman Instrument Inc., Fullerton, Calif.). The standard curve was used to determine the TNC of experimental samples.

Statistical analyses were performed using the SAS General Linear Models procedure (SAS Institute, 1987). Analyses of variance were conducted to evaluate main and interaction effects of the three treatment factors, and mean separation was performed using Fisher's LSD with α = 0.05.

Results and Discussion

Creeping bentgrass root dry weights were not affected by temperature, moisture, or soil CO₂ injection levels; however shoot dry weight differences due to temperature regimes were detected (Table 2). Mean shoot dry weights were 65% greater for 29.5/24 °C and 48% greater for 26.5/21 °C than for the 32/26.5 °C day/night temperatures (Table 3). Based on previous research (Krans and Johnson, 1974; Dipaola and Beard, 1992; Huang et al., 1998a,

Table 1. Gas composition of soil injections used on creeping bentgrass.

Soil injection	Gas composition (%)		
	O ₂	CO ₂	N ₂
High CO ₂	10.00	10.00	80.00
Low CO ₂	15.00	5.00	80.00
Air	20.94	0.03	78.09
Control	---	---	---

Table 2. Main and interaction effects of temperature, soil CO₂, and soil moisture on creeping bentgrass shoot and root dry weights, total nonstructural carbohydrates (TNC) in shoots and roots, net photosynthesis, and dark respiration.

Source of variation	df	Mean square					
		Shoot dry wt	Root dry wt	Shoot TNC	Root TNC	Net photosynthesis	Dark respiration
Temperature (T)	2	3.89**	3.91	6991.6*	1529.2*	8362.0**	438.9
CO ₂	3	0.20	0.28	503.3	5.6	1107.4**	1258.2*
T × CO ₂	6	0.14	0.43	350.3	8.3	877.1**	137.1
Moisture (M)	2	0.12	0.32	19.3	35.1	3.8	34.0
T × M	4	0.08	0.39	98.9	16.0	70.1	51.6
CO ₂ × M	6	0.02	0.23	59.2	30.3	66.4	27.9
T × CO ₂ × M	12	0.14	0.41	78.8	0.1	58.2	27.6

**Significant at P < 0.05 or 0.01, respectively.

Table 3. Effect of day/night temperature regimes and soil on creeping bentgrass shoot dry weights and total nonstructural carbohydrates (TNC) in shoots and roots.

Day/night temp °C	Shoot dry wt (g)	TNC (mg·g ⁻¹)	
		Shoot	Root
26.5/21	1.14	57.0	32.3
29.5/24	1.02	70.5	31.0
32/26.5	0.69	51.3	23.8
LSD _(0.05)	0.217	12.87	6.49

1998b), shoot dry weights were expected to be lowest for 32/26.5 °C due to decreased carbon assimilation reported for bentgrass at temperatures above 30 °C.

Bentgrass shoot and root TNC contents were affected by day/night temperature regimes but not by soil CO₂ or moisture levels (Table 2). Shoot TNC was greater for the 29.5/24 °C temperature regime (70.5 mg·g⁻¹) than for 26.5/21 °C (57.0 mg·g⁻¹) or 32.0/26.5 °C (51.3 mg·g⁻¹) (Table 3), while root TNC was greater for 26.5/21 °C (32.3 mg·g⁻¹) and 29.5/24 °C (31.0 mg·g⁻¹) than for 32/26.5 °C (23.8 mg·g⁻¹). Shoot and root TNC contents were expected to be highest for the lowest temperature regime based on previous research (Liu and Huang, 2000).

Interaction between temperature regimes and soil CO₂ injection levels was detected for net photosynthesis (Table 2). Net photosynthesis was greater for the 29.5/24 °C day/night temperature regime than for 32/26.5 °C at all soil CO₂ levels except 0.03% (Table 4). Net photosynthesis was unaffected by soil CO₂ injection levels when the 26.5/21 °C or 29.5/24 °C temperature regimes were used and averaged 10.8 and 18.5 μmol CO₂/m²/s, respectively. However, significant differences among soil CO₂ injection levels occurred for the 32/26.5 °C temperature regime, and net photosynthesis generally declined as soil CO₂ increased. Net photosynthesis was negative for 5% and 10% CO₂ (-2.69 and -20.21 μmol CO₂/m²/s, respectively), indicating respiration exceeded photosynthesis for these soil CO₂ levels under heat stress conditions.

Similar results were found by Xu and Huang (2000a, 2000b) with negative bentgrass photosynthetic rates after extended (>40 d) exposure to 35 °C. They also reported that reductions in net photosynthesis from increased temperature were amplified by high soil CO₂ concentrations. Chang and Loomis (1945) inferred that the effect of high soil CO₂ levels on photosynthesis may be due to interference with nutrient uptake. Williamson (1964) reported that a reduction in soil O₂ can decrease nutrient uptake. Lower soil O₂ levels that occur with increased soil CO₂ in a field setting were simulated by the gas injection levels in this study. High soil CO₂ or low soil O₂ levels could reduce photosynthesis capacity by limiting reactions occurring in the chloroplasts due to limited nutrient resources.

Dark respiration was affected by soil CO₂ injection levels (Table 2) and generally increased as CO₂ increased (Table 4). Dark respiration was greatest (22.20 μmol CO₂/m² s) for 10% CO₂, while 0.03% CO₂ and the control had lowest dark respiration rates (11.32 and 13.32 μmol CO₂/m² s, respectively). Negative net photo-

Table 4. Effect of day/night temperature regimes and soil CO₂ levels on creeping bentgrass net photosynthesis and effect of soil CO₂ levels on creeping bentgrass dark respiration.

Soil CO ₂ injection (%)	Net photosynthesis (μmol CO ₂ /m ² /s)			Dark respiration (μmol CO ₂ /m ² /s)
	Day/night temp regime			
	26.5/21 °C	29.5/24 °C	32/26.5 °C	
10.0	9.8	17.3	−20.2	22.2
5.0	10.6	20.6	−2.7	17.6
0.03	12.8	16.7	7.7	11.3
control	10.2	19.4	4.2	13.3
LSD(0.05) ^z	NS	NS	9.37	5.47

^aFor comparison of temperature regimes within a soil CO₂ injection level, LSD(0.05) = 11.27.

NS Nonsignificant.

synthesis at high soil CO₂ levels for the 32/26.5 °C temperature regime reflects respiration rates exceeding gross photosynthesis. This indicates that bentgrass was consuming carbohydrates faster than they were being produced under high temperature stress and high soil CO₂ levels, a deficit which eventually leads to decline in turf growth as carbohydrates are depleted. Huang and Gao (2000) reported similar results for creeping bentgrass grown at 34 °C.

Although shoot TNC results were contrary to previous studies, net photosynthesis and dark respiration results were consistent with published findings. Net photosynthetic rates of creeping bentgrass were generally lowest for the 32/26.5 °C day/night temperature regime, and net photosynthesis declined rapidly as soil CO₂ increased at this temperature regime. Respiration exceeded gross photosynthesis for 5% and 10% CO₂ at 32/26.5 °C indicating a carbon deficit caused by high temperature and high soil CO₂ levels. Soil moisture levels did not affect creeping bentgrass growth. In summary, this study revealed an imbalance between respiration and photosynthesis of creeping bentgrass at high temperatures and high soil CO₂ concentrations. Decline in bentgrass growth and quality are inevitable when respiration exceeds photosynthesis. Therefore, identifying means of increasing the photosynthetic capacity of bentgrass by preventing soil CO₂ from reaching high concentrations would be invaluable for managing creeping bentgrass under heat stress conditions.

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