THE INFLUENCE OF ENVIRONMENTAL VARIABLES ON CO_2 EXCHANGE RATES OF THREE COOL SEASON TURFGRASSES

ABSTRACT

Carbon dioxide exchange rates (CER) for Kentucky bluegrass (*Poa pratensis* L. cv. 'Magestic'), creeping bentgrass (*Agrostis palustris* Huds. cv. 'Penncross') and annual bluegrass (*Poa annua* var. *reptans* (Hausskn.) Timm.) were determined with an open gas analysis system. CER was measured under varying levels of light, temperature, ambient CO_2 concentration and leaf to air vapor pressure deficits (VPD). Diurnal effects for net assimilation were also determined. Light saturation for Kentucky bluegrass was near 500 μmol m^{-2} s^{-1}, while saturation for annual bluegrass and creeping bentgrass was near 1000 μmol m^{-2} s^{-1}. Maximum CER ranged from 14-33 °C for Kentucky bluegrass, 14-23 °C for creeping bentgrass and 15-17 °C for annual bluegrass. Dark respiration between 20 to 35 °C, increased 1.7, 2.0, and 2.8 times for Kentucky bluegrass, creeping bentgrass and annual bluegrass, respectively. Based on the average of the maximum CER from light and temperature data, Kentucky bluegrass had a net assimilation 30% higher than annual bluegrass and 47% higher than creeping bentgrass. Net assimilation for annual bluegrass was 25% higher than creeping bentgrass. Kentucky bluegrass, creeping bentgrass and annual bluegrass had CO_2 compensation points of 46, 84, and 74 µL L^{-1}, respectively. Within the range of VPD tested (0.5-1.0 KPa) no effect on CER was exhibited for all species evaluated. No diurnal effect on net assimilation was exhibited by any of the species tested. In general the three species tested exhibited responses typical of C_3 metabolism.

INTRODUCTION

Investigations into carbon dioxide exchange rates (CER) of plants has received a great deal of attention in most of the production oriented plant science disciplines. One discipline which lacks a fundamental base of characterization work is Turfgrass Science. The comprehensive bibliography on turfgrass literature compiled by Beard et al. (2) lists 30 references under the index heading of photosynthesis, yet only seven of these citations are scientific journal articles dealing specifically with turfgrass photosynthesis. The remainder are popular or semi-popular articles, dissertations, thesis or journal articles dealing with forage grass species which are also utilized as turf. A review of the literature since publication of this bibliography identifies current research in turfgrass photosynthesis, but fundamental characterization work is still lacking. A comprehensive identification of measurement conditions optimal for photosynthesis provides a base for further turfgrass assimilation research by identifying conditions which will maximize possible imposed treatment differences. The objectives of this research were to characterize the CO_2 exchange response of Kentucky bluegrass, creeping bentgrass and annual bluegrass in relation to light, temperature, CO_2, leaf to air vapor pressure deficit (VPD) and diurnal effects.

METHODS AND MATERIALS

Plant Material. Cores 2.5 cm in diameter were obtained from mature stands of annual bluegrass and creeping bentgrass located at the Hancock Turfgrass Research Center, East Lansing, MI. Tillers of Kentucky bluegrass were obtained from mature sod. Plants were transplanted into styrofoam cups and grown under 14 h photoperiods in a growth chamber with a 26 °C day and 16 °C night temperature. Photosynthetic photon flux (PPF) at turfgrass mid-canopy was 550-580 µmol m^{-2} s^{-1}. Plants were fertilized and watered as needed. All plants were preconditioned a minimum of two weeks in the growth chamber prior to gas exchange determinations.

Gas Exchange Measurements. All measurements were obtained in an open gas analysis system previously described by Augustine et al. (1) as modified by Sams and Flore (12). This system allows for the control and measurement of light intensity, temperature, ambient CO_2 and vapor pressure deficit (VPD). Measurements were made on 5-15 leaves placed into the assimilation chamber such that leaf to leaf shading was minimal. Immature and senescing leaves were excluded to ensure maximum gas exchange. The system consisted of four assimilation chambers allowing for four replications at each treatment level.

Light response curves were determined by exposing leaves to saturating PPF and subsequently increasing or decreasing the PPF in 30-100 μmol m^{-2} s^{-1} increments. Light intensity was varied by raising the chamber to the light source or by excluding light with neutral density filters. Temperature response curves were determined by measuring gas exchange after initially exposing the plant material to 20 °C. Leaf temperature was subsequently decreased stepwise to 7-10 °C and then increased to 35-40 °C in 7-10° C increments. Dark respiration temperature response was determined identically except all light was excluded from the assimilation chamber. Vapor pressure deficit was not controlled during temperature response determinations and ranged from 0.3 KPa at low temperatures to 4.7 KPa at high temperatures.

The response to differing levels of CO_2 was obtained by exposing plant material to low CO_2 concentrations (80-150 μL L^{-1}) and subsequently increasing concentration to 450-500 μL L^{-1} in 50 -75 μL L^{-1} increments. CO_2 compensation points were determined from linear regression between ambient CO_2 and CO_2 assimilation.

Data for diurnal effects were obtained by measurement of CO_2 assimilation periodically from 07:30 to 18:00 hrs.

VPD effects were determined by initially exposing plants to low VPD (0.4-0.5 KPa.) and subsequently increasing VPD. Because of physical problems with the system (see Discussion) deficits greater than 1 KPa were not measured.

Unless otherwise noted, all measurements were obtained at saturating light intensity (> 1000 mol s^{-1} m^{-2}), chamber temperature of 21 °C, ambient CO_2 concentration of 320-345 µL L^{-1} and a leaf to air vapor pressure deficit of < 1 KPa. Plant material was allowed to equilibrate at least 1 hr under the respective initial treatment level before measurement was made. Following a change in treatment level plant material was allowed to equilibrate until the CO_2 differential stabilized at ± 1 L L^{-1}.

Net assimilation and dark respiration were calculated as molar fluxes using the mole fraction of CO_2 as suggested by Cowen (5). Calculations were performed using computer programs designed by Moon and Flore (7). The maximum CER obtained for a given chamber was used to normalize data as a percent of maximum. All data were fitted with appropriate linear and non-linear regression models. Models were chosen based on best minimization of residual sums of squares and highest R^2. All regression analysis was performed by PlotIT (Scientific Programming Enterprises, Haslett, MI).

RESULTS AND DISCUSSION

Light Response. Photosynthetic rate for all three species increased with increasing light intensity until saturation (Figure 1). Saturation for Kentucky bluegrass was between 500-600 μmol m^{-2} s^{-1} while saturation for creeping bentgrass and annual bluegrass appeared to be near 1000 μmol m^{-2} s^{-1}. Pammentor et al. (10) reported saturation for creeping bentgrass to be about 500 μmol m^{-2} s^{-1} in a creeping bentgrass selection from a sub-antarctic island. Previous work on annual bluegrass and Kentucky bluegrass light response is not available. The three species tested exhibited a light response typical of C$_3$ metabolism (11).

Temperature Response. Net assimilation for all species increased with increasing temperature to an optimum and then declined (Figure 2). Chamber maximums ranged from 14-33 °C, for Kentucky bluegrass, 15-23 °C for creeping bentgrass and 14-17 °C for annual bluegrass. Optimal temperature for photosynthesis has been reported to be between 15-25 °C for creeping bentgrass (6,10,13). Because the VPD was not held constant as temperature was increased it is not possible to separate the high temperature effect on net assimilation from the effects of high VPD. Although separation of these effects may be of interest, in a field situation an increase in temperature would also increase VPD so the combined effect of these two parameters is still important.

The effect of temperature on dark respiration displayed a linear response for Kentucky bluegrass and creeping

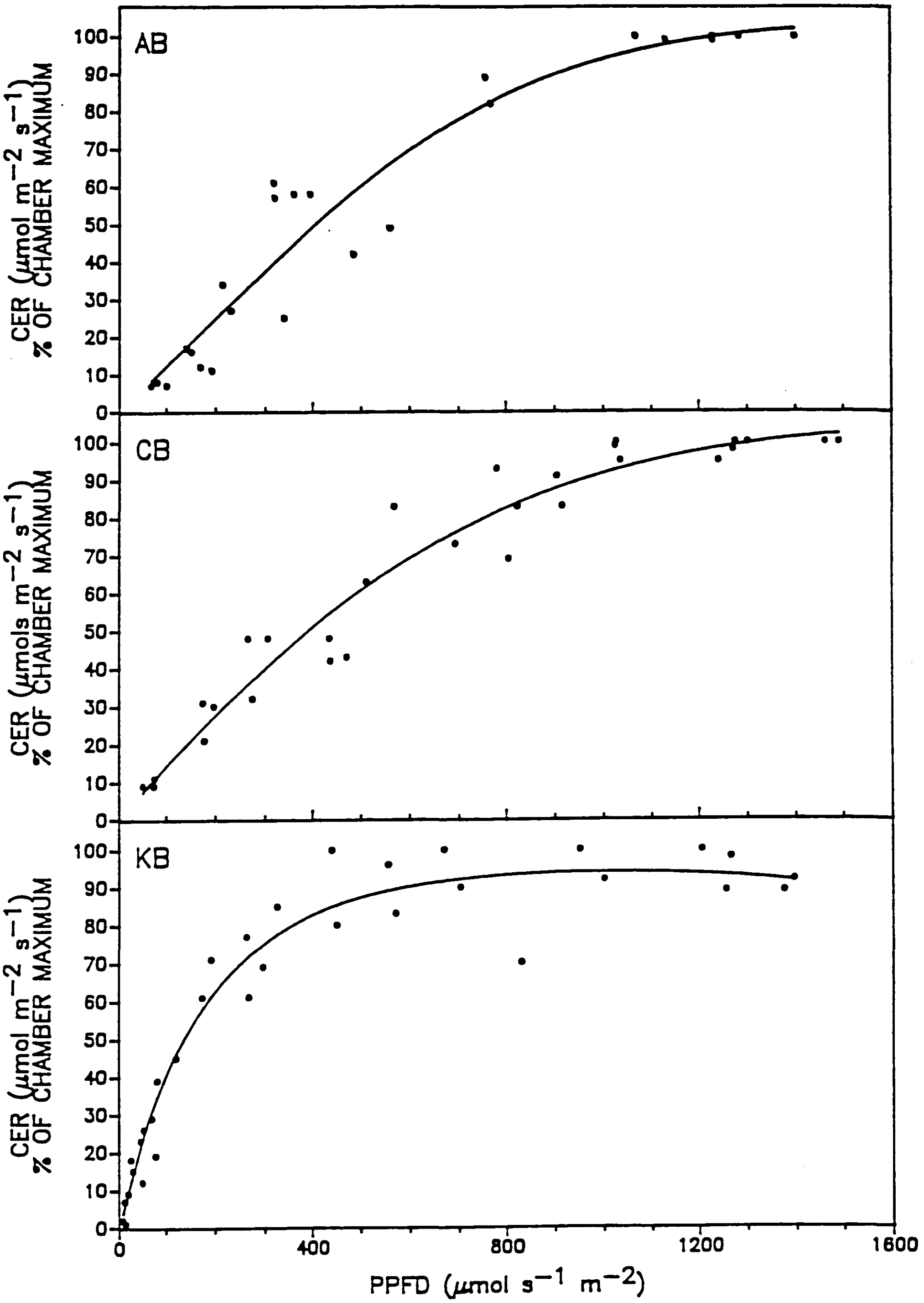

Figure 1. Effect of photosynthetic photon flux (PPF) on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB, $R^2=0.95$), creeping bentgrass (CB, $R^2=0.95$)and annual bluegrass (AB, $R^2=0.92$). Measurements were made at chamber temperature of 21°C and atmospheric CO_2 concentrations.

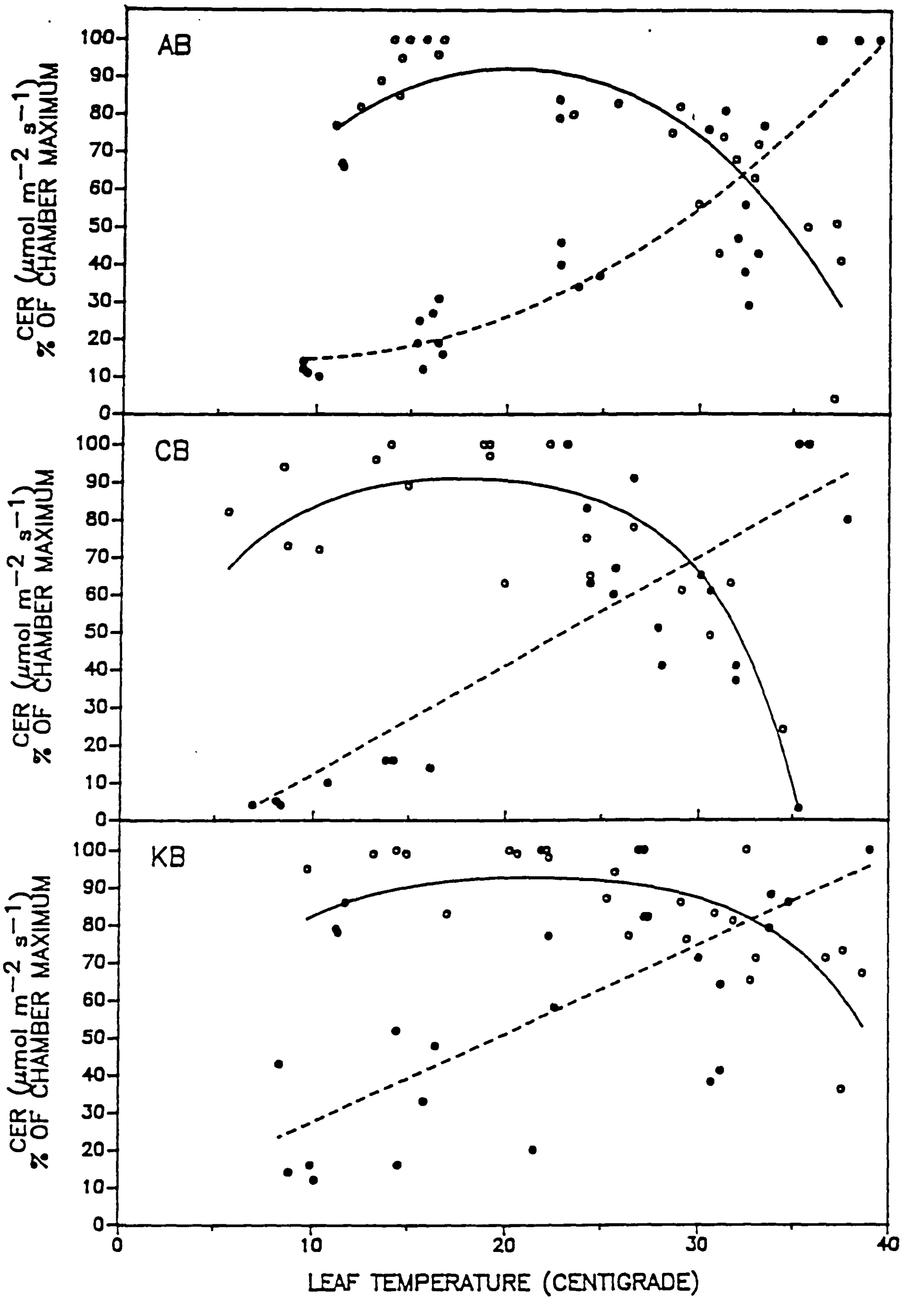

Figure 2. Effect of leaf temperature on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB), creeping bentgrass (CB) and annual bluegrass (AB). Net photosynthesis (solid line, open circle) measured at >1000 umol m^{-2} s^{-1} light intensity. CER and dark respiration (dashed line, closed circle) measured at atmospheric CO_2 concentrations. R^2 for KB, CB, and AB in the light, 0.48, 0.78, and 0.70 and in the dark, 0.49, 0.65, and 0.79, respectively.

bentgrass and a curvi-linear response for annual bluegrass with the steepest portion of the curve occurring at high temperatures (Figure 2). High temperatures impair the growth of cool season turfgrasses (3). The decrease in growth at high temperature can be due to an imbalance between metabolic processes which differ in their Q_{10}. One of these imbalances can occur because the optimal temperature for photosynthesis is lower than that of respiration. This results in a decrease in net assimilation as temperature increases. This response is evident in Figure 2. Because of a possible net assimilation/ respiration imbalance prolonged high temperatures could result in excessive carbohydrate depletion and death of the plant. Annual bluegrass is generally classified as being relatively heat intolerant (3,4,14) and the pronounced assimilation/ respiration imbalance at high temperature for this species may partially account for the low heat tolerance of annual bluegrass. Kentucky bluegrass and creeping bentgrass are more heat tolerant than annual bluegrass and exhibit less severe increases in dark respiration at high temperature. Wilkinson et al. (16) investigated photosynthetic-respiratory responses of Kentucky bluegrass and red fescue (*Festuca rubra* L.) and reported that dark respiration of red fescue was reduced at low light intensity while the dark respiration of Kentucky bluegrass was not, which may partially account for the relatively high shade tolerance of red fescue. The relationship between turfgrass heat tolerance and respiration/assimilation imbalance warrants further investigation.

CO_2 Response. Net assimilation increased with increasing ambient CO_2 concentration for all three species (Figure 3). All three species tested exhibit C_3 metabolism and increased levels of CO_2 should increase assimilation. Assimilation in C_3 species is stimulated by high levels of CO_2 because the increase in CO_2 inhibits photorespiration by increasing the ratio of CO_2 to O_2 reacting with ribulose diphosphate carboxylase (11). However CO_2 enrichment of turfgrass installations is not, as yet, feasible (3).

Diurnal and VPD Response. Results of linear regression analysis for diurnal and VPD effects are shown in Table 11. The low R^2 and non-significant F test ($P=0.01$) for diurnal effects indicates that the relationship between time of day and net assimilation is weak and measurement of CER, under the conditions tested is independent of time of day. Annual ryegrass (*Lolium multiflorum* Lam.) has been shown to exhibit diurnal fluctuations in net assimilation, but the fluctuation was closely associated with diurnal variability in ambient CO_2 concentrations (9). The CO_2 concentration within the assimilation chamber used in our experiments remained fairly constant ($\pm$ 5 $\mu L\ L^{-1}$) during the measurement period and should not have influenced net assimilation.

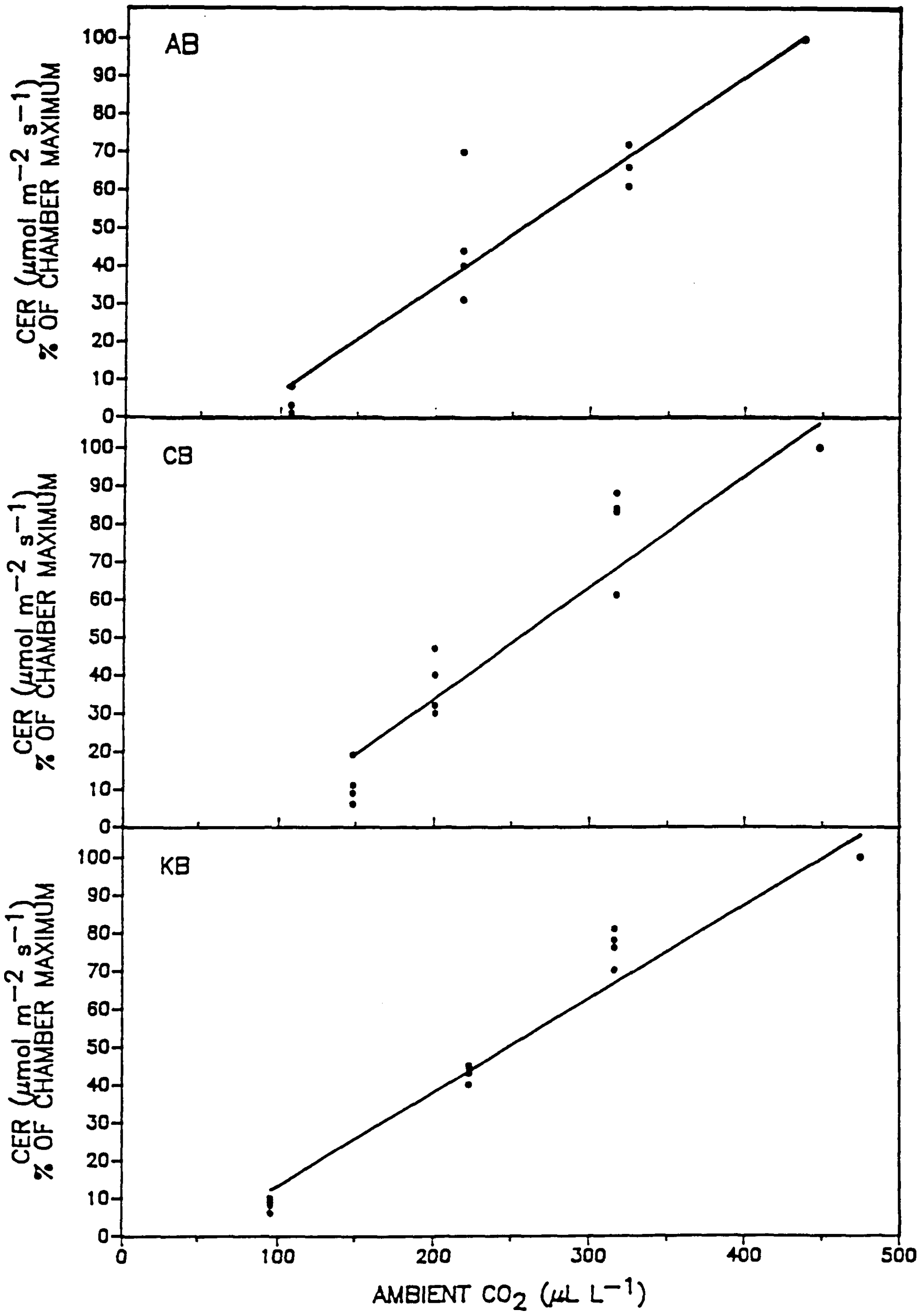

Figure 3. Effect of ambient CO_2 concentration on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB), creeping bentgrass (CB) and annual bluegrass (AB). All measurements obtained at >1000 umol m^{-2} s^{-1} light intensity and chamber temperature of 21°C. $R^2 = 0.97$, 0.92, and 0.93 for KB, CB, and AB, respectively.

No effect on CER to increasing VPD was seen for any of the species tested (Table 11). However the range of VPD tested (0.5-1.0 KPa) were probably not severe enough to affect assimilation. Woledge and Parsons (17) measured decreased photosynthesis in perennial ryegrass (*Lolium perenne* L.) when the water vapor saturation deficit of the ambient air was 6.0 g cm^{-3}. Moon et al. (8) reported a linear decrease in net assimilation with increasing VPD in blueberry when tested from 0.5 to 3.5 KPa. The original intent of our research was to test in the same range of VPD but several experimental problems made increasing the VPD in the assimilation chamber difficult. The system utilized for this investigation alters the vapor pressure of the air coming into the chamber by saturating the chamber air stream

Table 11. Summary of linear regression statistics for diurnal and vapor pressure deficit (VPD) effects on net photosynthesis of Kentucky bluegrass, creeping bentgrass, and annual bluegrass.

SPECIES	DIURNAL EFFECTS+			VPD EFFECTS++		
	R^2	$B_{(1)}$	F	R^2	$B_{(1)}$	F
Kentucky Bluegrass	0.032	0.173	1.23	0.185	-7.70	2.5
Creeping Bentgrass	0.048	0.098	1.90	0.121	-3.60	0.83
Annual Bluegrass	0.000	<0.001	<0.01	0.115	-2.99	0.78

Net photosynthesis measured at ambient temperature of 21° C at >1000 μmol m^{-2} s^{-1} light intensity.
+ Plants measured from 08:00 to 18:00 hours (n=39 for Kentucky bluegrass, 40 for creeping bentgrass, and 44 for annual bluegrass).
++Plants measured at leaf vapor pressure deficits from 0.5 to 1 KPa (n=16 for all species).

with water at a set temperature, lower than the temperature of the chamber heat exchanger. The dew point of the air is monitored before entering and after leaving the chamber. The outgoing dew point is used to determine the VPD, assuming 100% relative humidity within the leaf. The leaves within the chamber are actively transpiring and under field conditions this transpired water vapor would be readily diffused into the atmosphere. However, within the confines of the assimilation chamber the water vapor can increase the relative humidity and decrease VPD. In our studies the leaves of all three species increased the relative humidity enough to negate any VPD induced stress and the VPD within the chamber was maintained at < 1 KPa. This measurement problem might be circumvented by increasing the flow rate of the assimilation chamber or decreasing the set temperature of the incoming saturated air stream with an ethanol/water ice bath.

Species Comparison. Gas exchange parameters for species tested are summarized in Table 12. Based on the average of maximum assimilation values for light and temperature response curves, Kentucky bluegrass exhibited a CER 30% higher than annual bluegrass and 47% higher than creeping bentgrass. CER for annual bluegrass was 25% higher than creeping bentgrass. Dark respiration from 20 to 35 °C was increased nearly 3-fold for annual bluegrass, while the increase for Kentucky bluegrass and creeping bentgrass is approximately double. Creeping bentgrass had the highest

CO_2 compensation point while Kentucky bluegrass had the lowest. The compensation point of 46 L L^{-1} for Kentucky bluegrass is comparable to values previously reported for this species (15).

Table 12. A comparison of CO_2 gas exchange characteristics between Kentucky bluegrass (KB), creeping bentgrass (CB) and annual bluegrass (AB).

Gas Exchange Parameter	KB	CB	AB
Net Assimilation (mol m^{-2} s^{-1})$^{+}$	19.9	10.5	14.0
Dark Respiration (% of maximum)$^{++}$			
@ 20 °C	50	41	27
@ 35 °C	86	84	76
CO_2 Compensation Point (L L^{-1})$^{+++}$	46	84	74

+ Determined from maximum assimilation values of light response curves and temperature response curves.
++ Determined from dark respiration regression at 20 and 35 °C, respectively.
+++ Determined from linear regression between ambient CO_2 and CO_2 assimilation.

Results of this investigation indicated that the species tested exhibited responses to light, temperature and CO_2 typical of plants with C_3 metabolism (11). The response of these species to increasing VPD and temperature induced assimilation/respiration imbalances warrant further investigation.

REFERENCES

1) Augustine, J., M.A. Stevens, R.W. Breidenbach and D.F. Paige. 1976. Genotypic variation in carboxylation of tomatoes. Plant Physiol. 57:325-333.

2) Beard, J.B., H.J. Beard and D.P. Martin. 1977. Turfgrass bibliography. Mich. State Univ. Press. East Lansing MI.

3) Beard, J.B. 1973. Turfgrass:Science and culture. Prentice-Hall, Inc. Englewood Cliffs, NJ.

4) Beard, J.B., P.E. Rieke, A.J. Turgeon and J.M. Vargas. 1978. Annual Bluegrass *(Poa annua* L.) description, adaptation, culture and control. Res. Rpt. 352. Michigan State Univ. Agric. Exp. Sta., East Lansing, MI. 31 pp.

5) Cowen, I.R. 1977. Stomatal behavior and environment. Adv. Bot. Res. 4:117-228.

6) Miller, V.J. 1960. Temperature effect on the rate of apparent photosynthesis of Seaside bent and bermudagrass. Am. Soc. Hort. Sci. 75:700-703.

7) Moon, J.W. and J.A. Flore. 1986. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in a gas exchange system. Photosynthesis Res. 7:269-279.

8) Moon, J.W., J.A. Flore and J.F. Hancock. 1987. A comparison of carbon and water vapor gas exchange characteristics between a diploid and highbush blueberry. J. Amer. Soc. Hort. Sci. 112:134-138.

9) Murata, Y. and J. Iyama. 1963. Studies on the photosynthesis of forage crops. I. Diurnal changes in the photosynthesis of several grasses and barley seedlings under constant temperature and light intensity. Proc. Crop Sci. Soc. Japan. 31:311-314.

10)Pammentor, N.W., P.M. Drennan and V.R. Smith. 1986. Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-antarctic island. New Phytol. 102:143-160.

11)Salisbury, F.B. and C.W. Ross. 1978. Plant physiology. Wadsworth Pub. Co. Belmont, CA.

12)Sams, C.E. and J.A. Flore. 1982. The influence of age, position, and environmental variables on net photosynthesis of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

13)Schmidt, R.E. and R.E. Blaser. 1967. Effect of temperature, light, and nitrogen on growth and metabolism of 'Cohansey' bentgrass (*Agrostis palustris* Huds.) Crop Sci. 7:447-451.

14)Turgeon, A.J. 1985. Turfgrass management. Reston Pub. Co. Reston, VA.

15)Watschke, T.L., R.E. Schmidt, E.W. Carson and R.E. Blaser. 1973. Temperature influence on the physiology of selected cool season turfgrasses and bermudagrass. Agron. J. 65:591 -594

16)Wilkinson, J.F., J.B. Beard and J.V. Krans. 1985. Photosynthetic-respiratory responses of 'Merion' Kentucky bluegrass and 'Pennlawn' red fescue at reduced light intensities. Crop Sci. 15:165-168.

17)Woledge, J. and A.J. Parsons. 1986. The effect of temperature on the photosynthesis of ryegrass canopies. Ann. Bot. 57:487-497.