L

This is to certify that the

dissertation entitled

SPECIES DOMINANCE IN MIXED STANDS OF
CREEPING BENTGRASS AND ANNUAL BLUEGRASS

presented by

Roch Edmund Gaussoin

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Crop & Soil Sciences

Bruce Branham
Major professor

Date 2-23-1988

SPECIES DOMINANCE IN MIXED STANDS OF CREEPING BENTGRASS AND ANNUAL BLUEGRASS

By

Roch Edmund Gaussoin

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

1988

ABSTRACT

SPECIES DOMINANCE IN MIXED STANDS OF CREEPING BENTGRASS AND ANNUAL BLUEGRASS

By

Roch Edmund Gaussoin

Studies were conducted to determine factors which influence species dominance in mixed stands of annual bluegrass (*Poa annua* var. *reptans* (Hausskn.) Timm) and creeping bentgrass (*Agrostis palustris* Huds.).

A field study indicated that initial annual bluegrass population significantly influenced final populations. Returning clippings increased annual bluegrass 12% over clipping removed treatments. Daily irrigation, when not overseeded, increased annual bluegrass 8% over overseeded plots. High N-fertility, in combination with mefluidide, increased annual bluegrass populations 8% over control or EL-500 treatments. Clipping removed plots contained 60% less viable annual bluegrass seeds and 29% less soil K than clipping returned plots.

The encroachment of creeping bentgrass into annual bluegrass following application of nine different rates and timings of EL-500 was evaluated. After two years of data

collection no significant change in the spread of creeping bentgrass into annual bluegrass could be attributed to EL-500 treatments.

EL-500 at rates of 0.56 kg ha^{-1} or greater significantly inhibited the germination of annual bluegrass and creeping bentgrass, when applied at seeding. Inhibition of germination with increasing rates ranged from 8 to 50%.

Net photosynthesis of annual bluegrass, creeping bentgrass and Kentucky bluegrass (*Poa pratensis* L.) were characterized under varying environmental conditions. Light saturation was near 500 µmol m^{-2} s^{-1} for Kentucky bluegrass, and 1000 µmol m^{-2} s^{-1} for creeping bentgrass and annual bluegrass. Temperature range for maximum photosynthesis was 14-33, 14-23, and 15-17 °C for Kentucky bluegrass, creeping bentgrass and annual bluegrass, respectively. Dark respiration between 20 and 35 °C increased 1.7, 2.0 and 2.8 times for Kentucky bluegrass, creeping bentgrass and annual bluegrass, respectively. Photosynthesis of Kentucky bluegrass was 47% higher than creeping bentgrass and 30% higher than annual bluegrass, while annual bluegrass was 25% higher than creeping bentgrass.

El-500 inhibited photosynthesis of annual bluegrass and creeping bentgrass 58% 16 days after treatment (DAT). Mefluidide inhibited photosynthesis 44% 4 DAT and 55% 8 DAT. Mefluidide and EL-500 increased total chlorophyll 80 and 51%, respectively, 16 DAT. Increasing rates of EL-500 decreased photosynthesis of annual bluegrass 38%, while creeping bentgrass was unaffected by increasing EL-500 rates.

to brothers lost,

MARTIN AND DIRK

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to his major professor, Bruce Branham, for encouragement, guidance and advice. Also for allowing a Westerner to infiltrate the "Big 10".

Gratitude is also due to the members of the committee; Dr. Paul Rieke, Dr. Joe Vargas, and Dr. Jim Flore for their interest and support.

A special note of thanks to the Michigan Turfgrass Foundation and the United States Golf Association for financial support.

For help in the development of ideas, constructive criticism, and the stress relieving bitch sessions, thanks to fellow students, especially Jim Murphy and Bob Stovicek.

The author owes a debt of gratitude to his parents, Edmund and Dena, for spiritual, emotional and financial support when it was needed most.

Finally, but most importantly the author wishes to acknowledge the support, patience, understanding and sheet-warming of his wife Priscilla, and for things only a parent can understand, his daughter Sarah and son Travis.

TABLE OF CONTENTS

PHOTOSYNTHESIS AND CHLOROPHYLL CONTENT AS AFFECTED BY SYNTHETIC PLANT GROWTH REGULATORS

LIST OF TABLES

* Reprinted from HortScience 22:441-442. 1987

LIST OF FIGURES

INTRODUCTION

The following dissertation is a series of articles prepared for publication in various sources. The general research objective of these studies was to gain an understanding of factors involved in species dominance in mixed stands of creeping bentgrass (*Agrostis palustris* Huds.) and annual bluegrass (*Poa annua* var. *reptans* Hausskn. Timm.). Chapters One and Two were field investigations and Chapters Three, Five and Six were lab and greenhouse investigations. Chapter Four is a literature review pertaining to turfgrass photosynthesis. Each chapter contains an introduction explaining the chapter's objectives and pertinent literature. An extensive introduction would be redundant, therefore this introduction is brief and serves as a logical preface to the following chapters.

INFLUENCE OF CULTURAL FACTORS ON ANNUAL BLUEGRASS/CREEPING BENTGRASS INTERFERENCE

ABSTRACT

Research was conducted to determine the effect of five management factors and their interactions on the species composition of a mixed stand of annual bluegrass (*Poa annua* var. *reptans* (Hausskn.) Timm.) and creeping bentgrass (*Agrostis palustris* Huds.). Soil type was an Owosso-Marlette sandy loam complex (fine-loamy, mixed, mesic, Typic Hapludalfs). Management factors investigated were irrigation (daily at 75 % open pan evaporation (OPE), triweekly at 110 % OPE, and at wilt); clipping treatments (returned or removed); nitrogen fertility (98 or 293 kg ha^{-1} yr^{-1}); plant growth regulator (PGR) treatments (mefluidide at 0.14 kg ha^{-1}, EL-500 at 1.12 kg ha^{-1} and a control) and 'Penncross' bentgrass overseeding (49 kg ha^{-1} yr^{-1} or not overseeded). Treatment design was a 3 x 2 x 2 x 3 x 2 factorial. Treatments were applied for three years. Data were collected on change in annual bluegrass populations for each year and combined over three years. Data were also collected on clipping removal effects on annual bluegrass soil seed reservoir and P and K concentrations. Returning clippings increased annual bluegrass 12% over clippings removed plots. Daily irrigation, when not-overseeded increased annual bluegrass 8% over plots overseeded with creeping bentgrass. High nitrogen fertility in combination with mefluidide increased annual bluegrass populations over 8% compared to control or EL-500 plots at the same fertility level. The greatest significant decrease in annual bluegrass (28%) was in clippings removed, overseeded, non-PGR treated plots. Clippings removed plots had 60% less viable annual bluegrass seeds and 29% less soil K than clippings returned plots.

INTRODUCTION

Annual bluegrass (*Poa annua* L.) is a major grass component in most irrigated, close-cut, golf course fairways north of the transition zone (1,28). This is especially true on creeping bentgrass (*Agrostis palustris* Huds.) fairways which are maintained at clipping heights favorable for annual bluegrass (1,2,3). Annual bluegrass is normally not desirable but is present as an invasive species. The initial invasion of annual bluegrass occurs via annual bluegrass seed present in the soil or carried in by foot traffic or machinery (3,11,15). Once established annual bluegrass can, over time, become the dominant component of the turf stand (27).

Cultural practices have been found to influence the species dominance in mixed stands containing annual bluegrass. Engel (10) found cold weather applications of nitrogen to increase annual bluegrass in creeping bentgrass. Heavy spring nitrogen applications and activated sewage sludge when compared to urea or ammonium nitrate, have been found to encourage annual bluegrass encroachment into Merion Kentucky bluegrass (*Poa pratensis* L.) (1). Mahdi and Stoutemeyer (18) found increasing rates of nitrogen to decrease the invasion of annual bluegrass into a mixed stand of 'Merion' Kentucky bluegrass and 'Common' bermudagrass (*Cynodon dactylon* L.). Eggens and Wright (9) observed that, in polystand, the competitive ability of annual bluegrass was greater than 'Penncross' creeping bentgrass, but this competitive edge decreased as the ratio of NH_4^+ to NO_3^- increased. Waddington et al. (26) found annual bluegrass invasion was favored by P and K fertilization and the effect of one was enhanced by the other. Juska and Hanson (16) reported high levels of P to reduce the efficacy of preeemergence herbicides for annual bluegrass control. In a mixed stand of annual bluegrass and creeping bentgrass Goss (14) found a P rate of 86 kg ha^{-1} significantly increased annual bluegrass invasion and sulfur fertilization at 168 kg ha^{-1} produced better bentgrass turf with less annual bluegrass.

Sprauge and Evaul (23) found higher soil moisture levels were associated with more annual bluegrass. Youngner (29) reported high, frequent irrigations which maintained high soil moisture levels favored the persistence of annual bluegrass in bermudagrass turf in southern California. Decreasing irrigation levels during periods optimal for annual bluegrass growth has been found to deter encroachment (19).

Eggens (7) found no significant increase in Kentucky bluegrass after three years of overseeding an annual bluegrass fairway. Treatment of annual bluegrass fairways with mefluidide (N-[2,4-dimethyl-5 [[(trifluoromethyl) sulfonyl] amino] phenyl] acetamide) prior to overseeding has increased the success of perennial ryegrass (*Lolium perenne* L.) overseedings (8).

Removal of clippings from a polystand of annual bluegrass and Kentucky bluegrass can significantly suppress annual bluegrass invasion when compared to clippings returned treatments (1) . Pierce et al. (18) found clipping removal to significantly increase the creeping bentgrass population in a mixed stand of annual bluegrass and creeping bentgrass.

Breuninger and Watschke (5) determined that EL-500 (α -(1-methylethyl)- α -[4-trifluoro methoxy)phenyl] 5-pyrimidine methanol) significantly decreased the annual bluegrass population in perennial ryegrass, while mefluidide suppressed seedhead production but not populations of annual bluegrass. Shoop et al. (21) reported a significant visual decrease in annual bluegrass populations in an annual bluegrass/creeping bentgrass fairway after EL-500 treatment.

The literature indicates that cultural practices play a significant role in the persistence of annual bluegrass in mixed stands. However the literature is limited on the effects of cultural practices and particularly their interactions on the species composition of mixed stands of annual bluegrass and creeping bentgrass. The objectives of this research were to evaluate the effects of five management practices and their interactions on the species composition of a mixed stand of annual bluegrass and creeping bentgrass and to evaluate the effects of clipping removal on annual bluegrass soil seed reservoir and soil and plant tissue P and K nutrient levels.

MATERIALS AND METHODS

Research was conducted at the Hancock Turfgrass Research Center, East Lansing, MI on a mixed stand of annual bluegrass and creeping bentgrass. Plot size was 1.8 x 1.2 m. Fungicides and broadleaf herbicides were applied as needed to prevent broadleaf weed invasion and disease. Treatments were initiated in May of 1984 and terminated in October of 1986. Experimental design was a randomized complete block with three replications. Treatment design was a 3 x 2 x 2 x 3 x 2 factorial with two splits, with irrigation treatments as main plots, clipping removal treatments as subplots and nitrogen fertility, PGR and overseeding factors as sub-sub plots.

CULTURAL TREATMENTS

Irrigation treatments were started the first week in June and terminated the second week in September in all years of the study. Treatments were applied via sprinkler irrigation through quarter-circle heads which delivered 20 mm hr^{-1}. Two of the treatments were based on daily evaporation readings obtained from a Class A evaporative pan located adjacent to the treatment area. These treatments were daily irrigation at 75 % of open pan evaporation (OPE) and triweekly irrigation at 110% OPE. Rainfall was subtracted from the required irrigation amount prior to application. A third treatment was applied when the plots exhibited moderate to severe wilt symptoms (i.e. footprinting and/or a blueing of the plot area). Irrigation and rainfall amounts are shown in Table 1.

Clipping treatments consisted of mowing with (clippings removed) or without (clippings returned) the catch baskets on a triplex greens mower. Mowing frequency was three times per week with a height of cut of 13 mm (bench setting). Clipping treatments were started in early May and ended in late September of each year of the study.

Table 1. Irrigation and precipitation amounts for three irrigation treatments applied to annual bluegrass/creeping bentgrass interference study.

	IRRIGATION TREATMENT+											
	75%	110%	WLT	PPT	75%	110%	WLT	PPT	75%	110%	WLT	PPT
MONTH/YR	1984				1985				1986			
						------mm-----						
APRIL-MAY	0	0	0	171	0	0	0	164	0	0	0	143
JUNE	147	221	20	10	66	137	27	52	86	80	0	193
JULY	102	168	13	45	115	198	17	52	52	140	8	61
AUGUST	91	74	0	94	46	69	30	91	55	96	7	62
SEPT	48	28	0	77	0	33	0	93	18	0	0	208
TOTALS	388	491	33	397	227	437	74	452	211	316	15	667

+ Irrigation treaments; daily irrigation at 75% of open pan evaporation (OPE), 3 times per week at 110% of OPE and irrigation at wilt (WLT).

Nitrogen fertility treatments were 98 kg ha^{-1} yr^{-1} (low-N) and 293 kg ha^{-1} yr^{-1} (high-N) applied as urea (46-0-0). High-N treatments were applied monthly on the 15th of May through September and November at 49 kg ha^{-1} per application. Low-N treatments were applied the 15th of June, July, September and November at 24.5 kg ha^{-1} per application. Fertilizer carrier was urea (46-0-0).

PGR treatments consisted of mefluidide, EL-500 and a control. Mefluidide treatments were applied 15 May 1984, 30 April 1985, and 25 April 1986 at 0.14 kg ha^{-1}. Due to the late application timing in 1984 mefluidide treatments were applied with 0.5 % HA-89 surfactant. EL-500 treatments were applied 15 May 1984 at 1.68 kg ha^{-1} and 14 May 1985, and 30 April 1986 at 1.12 kg ha^{-1}. Treatments were applied with a hand held CO_2 sprayer calibrated to deliver 467 L ha^{-1} at 0.21 MPa.

In August of each year overseeding treatments were applied. The overseeding treatment was a broadcast overseeding of Penncross creeping bentgrass at 49 kg ha^{-1}. Prior to overseeding the experimental area was verticut with a triplex mower equipped with verticut reels. The verticut reels were set to a depth which cut through the turf and thatch but just lightly into the soil. Overseeding treatments were than applied and brushed in with a nylon bristle broom. Immediately after overseeding the area received 5 mm irrigation.

Data were obtained on the population of annual bluegrass in each plot. The annual bluegrass population was estimated by modification of the vertical point quadrat method described by Tinney et al. (24). A PVC frame 1.8 x 1.2 m with an internal monofilament grid of 112 intersections on 100 mm centers was placed over an individual plot. The presence of annual bluegrass under an intersection was recorded as a "hit". The number of hits per plot was divided by 112 and multiplied by 100 to obtain an estimate of the percentage annual bluegrass in each plot. The precision of this method was validated by recounts of randomly selected plots. At no time did the recounts deviate more than 5% from the original estimates. Initial population estimates were made in the spring of 1984 and yearly annual bluegrass population changes were calculated from counts obtained in the fall of 1984, 1985, and 1986. The change in annual bluegrass populations for each year and the sum of the population shift for three years were used in data analysis.

STATISTICAL ANALYSIS

To control error and increase precision in the analysis the initial annual bluegrass population estimates obtained in 1984 were used as a covariate and the experiment analyzed by analysis of covariance. Data were analyzed with SAS (Statistical Analysis System, SAS Institute Inc., Cary, NC), utilizing the General Linear Models procedure. Planned comparison of means were performed by orthogonal contrasts.

SEED RESERVOIR AND TISSUE AND SOIL P AND K CONCENTRATIONS

In November of 1985 and 1986 samples were obtained from the clipping treatments with a 91 cm^2 core sampler to a depth of 7.6 cm. In 1985 two samples per replication were obtained for each treatment (n=6). In 1986 three samples per replication were obtained for each treatment (n=9). The core samples were air-dried and broken up over a flat in the greenhouse. The flats were irrigated twice daily for four minutes with an automatic misting system. Temperature in the greenhouse fluctuated between 10° and 24° C. After 25 days the number of annual bluegrass plants in each flat were counted. Data were expressed as the number of viable annual bluegrass seeds per 100 gms soil, based on a soil bulk density of 1.5 gm cm^{-3}. Clipping treatments were compared using a Student's t test.

Clippings and soil samples were collected from the clipping treatments and analyzed for P and K. Clipping samples were obtained 6 June and 25 October, 1986. Soil

samples were taken 21 June, 1985 and 27 October, 1986 to a depth of 76 mm with a 25 mm diameter soil probe. Both clipping and soil samples were digested in nitric acid and analyzed for P and K using emission spectroscopy. Treatments were separated using a Student's t test.

RESULTS AND DISCUSSION

The results of the analysis of covariance are shown in Table 2. Main effects or interactions not shown were not significant at any time in the study. Discussion of results will be confined to significant yearly and combined year main effects and significant interactions for the combined year analysis.

Table 2. Analysis of covariance. Influence of cultural practices on annual bluegrass (*Poa annua* var. *reptans*) and creeping bentgrass (*Agrostis palustris*) interference

	YEAR			
	1984	1985	1986	COMB.
MAIN EFFECTS				
CLIPPING TRTMNTS (CR)	**	NS	*	**
N-FERTILITY (F)	NS	**	NS	NS
PLANT GROWTH REG (PGR)	NS	NS	NS	*
COVARIATE-INITIAL ANNUAL BLUEGRASS POPULATION	**	NS	NS	**
INTERACTIONS				
IRRIGATION (I) x CR	**	NS	NS	NS
I x OVERSEEDING (O)	*	NS	NS	*
I x F	NS	**	NS	NS
PGR x F	NS	NS	NS	*
PGR x F x CR	NS	NS	*	NS
O x I x CR x F	NS	*	NS	NS
O x PGR x CR	NS	NS	*	*

*, **, or NS indicate significance at P = 0.05, P = 0.01 and non-significant, respectively.

After three years, clipping removal significantly decreased the annual bluegrass population when compared to plots where clippings were returned. For individual years clipping removal reduced the annual bluegrass population in 1984 and 1986 but not in 1985 (Table 3). These results concur with the findings of others (1,20). Several explanations are possible for the clipping treatment response. Fales and Wakefield (12) observed that suppression of the growth of forsythia and flowering dogwood by three turfgrasses may involve chemical inhibition. Annual bluegrass clippings may contain allelo-chemicals which selectively inhibit the growth of creeping bentgrass or enhance the growth of annual bluegrass. Brede and Harris (4) reported that annual bluegrass seeds may secrete a water insoluble toxin which significantly inhibits creeping bentgrass seedlings. High P and K levels have been shown to favor annual bluegrass (26). Removing clippings decreases specific soil nutrient levels which may favor creeping bentgrass over annual bluegrass. Finally the prolific seed production of annual bluegrass (1) and its ability to produce viable seed on excised panicles (17) coupled with seed production throughout the growing season (11) indicate that the returning of clippings may, in effect, be annual bluegrass overseeding.

Nitrogen fertility significantly affected the annual bluegrass population in only one year of the three year investigation. In 1985 plots that received 98 kg ha^{-1} yr^{-1}

had significantly less annual bluegrass than plots which received 293 kg ha^{-1} yr^{-1} (Table 3). Beard et al. (1) and Waddington et al. (26) found urea treated plots to have less annual bluegrass than plots which received activated sewage sludge. The increase in the annual bluegrass in sewage sludge treated plots was postulated to be due to the P present in the sewage sludge and absent in the urea (26). Engel (10) reported that nitrogen fertility procedures were unlikely to be the major cause of the encroachment of annual bluegrass into creeping bentgrass in New Jersey.

PGR's did not significantly affect the annual bluegrass population in any one year of the study, but when the data were combined over all three years PGR's were a significant source of variability. In the combined year analysis mefluidide treated plots had significantly more annual bluegrass than either the control or EL-500 treated plots (Table 4). Mefluidide inhibits annual bluegrass seedhead production (5,6). Spring applications of mefluidide coincide with a period when annual bluegrass seedhead production is very high (11). After mefluidide applications, the assimilates and reserves normally allocated to seedhead production may be reallocated to other portions of the plant such as roots or crown tissue. In perennial ryegrass (*Lolium perenne* L.) flower production has been found to limit the initiation of main root axes (25). Soper (22) observed an increase in the summer survival of ryegrass (*Lolium* spp.) when the ratio of

Table 3. Main effect means for clipping and N-fertility treatments averaged across all other factors. (n= 108). Means for 1984 and combined year analysis are adjusted for the covariate (initial annual bluegrass population).

	YEAR			
	1984	1985	1986	COMBINED
	---annual bluegrass population (% change)---			
Clippings				
Returned	0.7	-7.5	-3.4	-10.0
Removed	-5.3	-8.1	-8.8	-22.1
N-Fertility				
98 kg ha^{-1} yr^{-1}	-2.0	-10.1	-4.8	-16.1
293 kg ha^{-1} yr^{-1}	-2.6	-6.2	-7.5	-16.1

Table 4. Main effect means for plant growth regulator treatments averaged across all other treatments (n = 72). Means for 1984 and combined year are adjusted for the covariate (initial annual bluegrass population).

	YEAR			
	1984	1985	1986	COMBINED
	---annual bluegrass population (% change)---			
PGR Treatment				
Mefluidide	-0.5	-8.4	-5.6	-13.4
EL-500	-3.3	-8.7	-4.9	-17.4
Control	-3.2	-7.3	-7.7	-17.5

Orthogonal comparisons for combined year adjusted means

	OSL[+]
Mefluidide vs Control	0.03
Mefluidide vs EL-500	0.03
EL-500 vs Control	0.96

[+] Observed significance level

vegetative to reproductive culms increased. Cooper et al. (6) found mefluidide treated annual bluegrass to have deeper roots and greater root elongation rates than untreated annual bluegrass. The inhibition of seedhead formation by mefluidide may increase the persistence of annual bluegrass by promoting new root initiation or reducing summer root deterioration.

Plots which were not overseeded and irrigated daily at 75% of OPE had significantly more annual bluegrass than the non-overseeded plots irrigated at 110% OPE 3 times per week or at wilt (Table 5). Continuous high soil moisture levels have been observed to encourage annual bluegrass (23,29). In this study the frequency of irrigation (daily vs. triweekly or at wilt) may have influenced the dominance of annual bluegrass more than irrigation amount. Daily irrigation maintains soil moisture levels in the upper regions of the soil profile at levels which may favor the existing annual bluegrass plants or germination of new plants from annual bluegrass seed present in the soil. Table 5 also shows that for bentgrass overseeding to be effective plots must be irrigated daily.

The response of mefluidide was significantly affected by N-fertility while the EL-500 and control treated plots were unaffected (Table 6). High N-fertility in combination with mefluidide increased annual bluegrass populations.

Table 7 displays the data for the PGR X Clipping Removal X Overseeding interaction for the combined year

Table 5. Irrigation x Overseeding interaction means for combined year analysis. Means are adjusted for covariate (initial annual bluegrass population).

	IRRIGATION TREATMENT+		
	75%	110%	WILT
	---annual bluegrass population (% change)---		
Overseeded++	-17.5	-14.1	-20.8
Non-Overseeded	-9.7	-15.6	-18.7

Orthogonal comparisons

	OSL+++
Non-Overseeded:	
75% vs 110%	0.03
75% vs WILT	<0.01
Overseeded vs Non-Overseeded:	
at 75%	<0.01
at 110%	0.56
at WILT	0.42

+ Irrigation treatments were: daily irrigation at 75% of open pan evaporation (OPE), 3 times per week at 110% of OPE and irrigation at wilt.

++ Plots were overseeded in mid-August with Penncross creeping bentgrass at 49 kg ha^{-1}

+++ Observed significance level

Table 6. Plant Growth Regulator x N-Fertility interaction means for combined year analysis.

Plant Growth Regulator	N-Fertility (kg ha^{-1} yr^{-1}) 98	293
	---annual bluegrass population (% change)---	
Mefluidide	-16.2	-10.6
EL-500	-15.4	-19.4
Control	-16.7	-18.3

Orthogonal comparisons:

	OSL+
Control:Low N vs High N	0.54
Mefluidide:Low N vs High N	0.04
EL-500:Low N vs High N	0.13
High N:	
Mefluidide vs Control	<0.01
Mefluidide vs EL-500	<0.01
EL-500 vs Control	0.67
Low N:	
Mefluidide vs Control	0.84
Mefluidide vs EL-500	0.76
EL-500 vs Control	0.62

+ Observed Significance Level

Table 7. Overseeding x Plant Growth Regulator x Clipping Treatment interaction means for combined year analysis. Means are adjusted for covariate (initial annual bluegrass population). Data represent % change in annual bluegrass populations.

	Plant Growth Regulator Treatment					
	Mefluidide		EL-500		Control	
Clipping Treatment+	C+	C-	C+	C-	C+	C-
Overseeding Treatment++	--annual bluegrass population (% change)--					
OS	-10.1	-20.5	-14.4	-23.3	-8.2	-28.4
Non-OS	-9.6	-13.3	-6.8	-25.1	-11.1	-22.2

Orthogonal comparisons:

	OSL+++	
Mefluidide: OS(C-) vs OS(C+)	<0.01	
Control:		
OS(C-) vs OS(C+)	<0.01	
Non-OS(C-) vs Non-OS(C+)	<0.01	
EL-500:		
OS(C-) vs OS(C+)	0.02	
Non-OS(C-) vs Non-OS(C+)	<0.01	
OS(C+) vs Non-OS(C+)	0.04	
	OS	Non-OS
Clippings Returned:		
Control vs EL-500	0.09	0.25
Control vs Mefluidide	0.39	0.67
Mefluidide vs EL-500	0.24	0.46
Clippings Removed:		
Control vs EL-500	0.18	0.44
Control vs Mefluidide	0.04	0.02
Mefluidide vs EL-500	0.47	<0.01

\+ C+ and C- designate clippings returned and clippings removed, respectively.

++ Overseeding treatments were overseeded (OS) in mid-August with Penncross creeping bentgrass at 49 kg ha^{-1} or not overseeded (Non-OS).

+++ Observed Significance Level

analysis. Within the control and EL-500 plots the clippings removed treatment, overseeded or not, had significantly less annual bluegrass than the corresponding clippings returned plots. However, the mefluidide plots exhibited the same clipping effect only when overseeded. Within the EL-500 clippings returned treatments, the overseeded plots had less annual bluegrass than the non-overseeded plots. The application of EL-500 may have suppressed the spring growth of the polystand enough to allow successful establishment of bentgrass from seed, or suppressed the spring germination of annual bluegrass seed present in the soil. EL-500 has been shown to exhibit preeemergence activity on both annual bluegrass and creeping bentgrass (13), when applied at time of seeding. Within the overseeded plots PGR applications had no effect in the clippings returned plots, but in the clippings removed plots the mefluidide treatments had significantly more annual bluegrass than the control plots. This was also true of the non-overseeded plots. The non-overseeded, clippings removed plots treated with EL-500 also contained less annual bluegrass than the corresponding mefluidide treated plots but did not differ from the corresponding control plots.

SEED RESERVOIR AND TISSUE AND SOIL P AND K CONCENTRATIONS

Clipping returned plots had significantly more viable annual bluegrass seeds than the clippings removed plots. In 1985 clippings returned plots had 42 viable annual bluegrass seeds per 100 gms of soil vs. 16 seeds per 100 gms for the clippings removed plots. In 1986 clipping returned plots contained 13 seeds per 100 gms of soil vs. 5 seeds per 100 gms of soil for the clipping removed plots. Although the amount of viable annual bluegrass seeds in the clipping removed plots is quite high, when averaged across years, these plots contained 60% less annual bluegrass seeds than the clippings returned plots. The difference between the two treatments should increase the establishment of annual bluegrass plants from seed in the clippings returned treatment. The data supports the hypothesis that the returning of clippings is a passive form of annual bluegrass overseeding.

Clipping removal significantly lowered the soil K levels when compared to clippings returned plots (Table 8). The K levels in tissue samples were also reduced by clipping removal on the 6 June, 1986 sampling date, but not on the samples obtained in October. Waddington et al. (26) found high K

Table 8. Clipping removal effects on tissue and soil P and K concentrations of an annual bluegrass creeping bentgrass polystand.

	Element							
	P	K	P	K	P	K	P	K
	Sample Date							
	6/6/86		10/25/86		6/21/85		10/27/86	
Clipping Treatment	Tissue				Soil			
	-----mg kg^{-1}----				-----kg ha^{-1}----			
Removed	488a	2451a	477a	1063a	133a	96a	74a	87a
Returned	509a	2751b	493a	1100a	129a	145b	75a	113b

Numbers within columns followed by different letters are significantly different based on a paired t test (P=0.05) levels to enhance the encroachment of annual bluegrass into creeping bentgrass. The reduction of K concentrations in the clipping removed plots may have been a factor in the reduction of annual bluegrass populations in the clipping removal plots. P levels in both the soil and tissue samples were unaffected by clipping removal.

The results of this investigation indicate that cultural practices can play a significant role in enhancing or detering the encroachment of annual bluegrass in close-cut creeping bentgrass. Clipping removal reduced the encroachment of annual bluegrass into creeping bentgrass and also reduced the reservoir of annual bluegrass seed in the soil and soil and plant tissue K concentrations. High N fertility increased annual bluegrass in one year of the study but did not prove to be a significant factor over time. Treatment with mefluidide, singly or in combination with high N fertility increased annual bluegrass populations. Overseeding was effective in increasing creeping bentgrass only when plots were treated with EL-500 or irrigated daily. However, daily irrigation without overseeding increased annual bluegrass. The numerous interactions observed indicate that the persistence of annual bluegrass can not be easily isolated to any one management practice but depends on the overall cultural program.

REFERENCES

1) 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.

2) Bogart, J.E. and J.B. Beard. 1973. Cutting height effects on the competitive ability of annual bluegrass (*Poa annua* L.). Agron. J. 65:513-514.

3) Brede, A.D. and J.M. Duich. 1981. Annual bluegrass encroachment affected by Kentucky bluegrass seeding rate. p.307-311 *In* Proc. 35th Annual Meeting Northeastern Weed Sci. Soc., Philadelphia, PA. 6-8 Jan. 1981. Evans Printing Inc. Salisbury, MD.

4) Brede, A.D. and T. Harris. 1987. Plant toxins and competition in annual bluegrass and bentgrass turfs. p. 123. *In* 57th Annual Mich. Turf. Conf. Proc. Lansing, MI. 12-14, January 1987. Mich. Turf. Found., Mich. Ag. Exp. Sta. and Coop. Ext. Service. Mich. State Univ. E. Lansing, MI.

5) Breuninger, J.M. and T.L. Watschke. 1982. Post emergent *Poa annua* control with growth retardants. p.314. *In* Proc. 36th Annual Meeting Northeastern Weed Sci. Soc. New York, NY. 5-7 Jan. 1982. Evans Printing, Inc. Salisbury, MD.

6) Cooper. R.J., P.R. Henderlong, J.R. Street, and K.J. Karnok. 1987. Root growth, seedhead production, and quality of annual bluegrass as affected by mefluidide and a wetting agent. Agron. J. 79:929-934.

7) Eggens, J.L. 1979. The response of some Kentucky bluegrass cultivars to competitive stress from annual bluegrass. Can. J. Plant Sci. 59:1123-1128.

8) Eggens, J.L. 1984. Fairway overseeding with Embark. Greenmaster. 6:17.

9) Eggens, J.L. and C.P.M. Wright. 1985. Nitrogen effects on monostands and polystands of annual bluegrass and creeping bentgrass. HortScience. 20:109-110.

10)Engel, R.E. 1974. Influence of nitrogen fertilization on species dominance in turfgrass mixtures. p. 104-111 *In* Proc. 2nd Int. Turfgrass Res. Conf. Blacksburg, VA. June 1973. Amer. Soc. Agron., Crop Sci. Soc. Amer. Madison, WI.

11)Engel, R.E. and R.D. Ilnicki. 1969. Turf weeds and their control. *In* A.A. Hanson and F.V. Juska (ed.) Turfgrass Science. Agronomy 14:240-287.

12)Fales, S.L. and R.C. Wakefield. 1981. Effects of turfgrass on the establishment of woody plants. Agron J. 73:605-610.

13)Gaussoin, R.E. and B.E. Branham. 1987. Annual bluegrass and creeping bentgrass germination response to flurprimidol. HortScience 22:441-442.

14)Goss, R.L. 1974. Effects of variable rates of sulfur on the quality of putting green turfgrass. p. 172-175. *In* Proc. 2nd Int. Turfgrass Res. Conf. June 1973. Amer. Soc. Agron., Crop Sci. Soc. Amer. Madison, WI.

15)Jagshitz, J.A. 1986. Establishment of turfgrass, crabgrass and annual bluegrass following herbicide use. p. 270-271. *In* Proc. 40th Annual Meeting Northeastern Weed Sci. Soc. Boston, MA. 7-9, Jan. 1986. Evans-Coates Printing, Inc. Salisbury, MD.

16)Juska, F.V. and A.A. Hanson. 1967. Factors affecting *Poa annua* L. control. Weeds 15:98-101.

17)Koshy, T.K. 1969. Breeding systems in annual bluegrass, *Poa annua* L. Crop Sci. 9:40-43.

18)Mahdi, Z. and V.T. Stoutmeyer. 1953. A method of measurement of populations in dense turf. Agron. J. 45:514-515.

19)Musser, H.B. 1962. Turf Managememt (Revised). McGraw-Hill Book Co. Inc. NY. pp. 1-356.

20)Pierce, N.L., J.L. Eggens and C.P.M. Wright. 1987. Mowing fairways with greensmowers. Greenmaster 2:7-11.

21)Shoop, G.L., R.H. Hoefer and D.G. Ortega. 1986. Flurprimidol (EL-500) growth regulator effect on bentgrass fairways in the northeast. p. 131. *In* Proc. 40th Annual Meeting Northeastern Weed Sci. Soc. Boston, MA. 7-9, Jan. 1986. Evans-Coates Printing, Inc. Salisbury, MD.

22)Soper, K. 1958. Effects of flowering on the root system and summer survival of ryegrass. N. Z. Jour. Agric. Res. 1:329-340.

23)Sprague, H.B. and G.W. Burton. 1937. Annual bluegrass (*Poa annua* L.) and its requirements for growth. New Jersey Agr. Expt. Sta. Bull. 630. pp. 1-24.

24)Tinney, F.W., O.S. Aamodt and H.L. Ahlgren. 1937. Preliminary report of a study on methods used in botanical analysis of pasture swards. Jour. Amer. Soc. Agron. 29:835-840.

25)Troughton, A. 1978. The influence of reproductive developement upon the root system of perennial ryegrass and some effects on herbage production. J. Agric. Sci. Cambridge. 91:427-431.

26)Waddington, D.V., T.R. Turner, J.M. Duich and E.L. Moberg. 1978. Effect of fertilization on Penncross creeping bentgrass. Agron. J. 70:713-718.

27)Watschke, T.L. and J.M. Duich. 1977. Control of *Poa annua* with endothal. p. 357-359 *In* Proc. 31st Meeting Northeastern Weed Sci. Soc. Baltimore, MD. 4-6, Jan. 1977. Evans Printing, Inc. Salisbury, MD.

28)Wilson, C.G. and J.M. Latham, Jr. 1969. Golf fairways, tees and roughs.*In* A.A. Hanson and F.V.Juska (ed.) Turfgrass Science. Agronomy 14:584-602.

29)Younger, V.B. 1959. Ecological studies on *Poa annua* in turfgrasses. J. British Grasslands Soc. 14:233-237.

ENCROACHMENT OF CREEPING BENTGRASS INTO ANNUAL BLUEGRASS FOLLOWING EL-500 TREATMENT

ABSTRACT

EL-500 (α-(1-methylethyl)- α -[4-trifluoro methoxy)phenyl] 5-pyrimidine methanol) is a synthetic plant growth regulator (PGR) developed for use on turfgrass. A field experiment was conducted to determine if, at different rates and timings EL-500 could enhance the encroachment of creeping bentgrass into annual bluegrass. The experiment was conducted in East Lansing,MI on a mature stand of annual bluegrass (*Poa annua* var *reptans* (Hausskn.) Timm.) into which cores of creeping bentgrass *(Agrostis palustris* Huds. cv. 'Penncross') were transplanted. Soil type was an Owosso-Marlette sandy loam complex (fine-loamy, mixed, mesic, Typic Hapludalfs). Nine EL-500 treatments were applied in 1985 and 1986. Creeping bentgrass encroachment was evaluated by measuring the area of the bentgrass cores with a planimeter from traces obtained in the field. Data was collected in the summer and fall of both years. After two years of data collection no significant change in the

spread of the creeping bentgrass could be attributed to EL-500 treatments. Results indicate that EL-500 was ineffective in enhancing the encroachment of creeping bentgrass into annual bluegrass.

INTRODUCTION

Mixed stands of *Poa annua* L. (annual bluegrass) and *Agrostis palustris* Huds. (creeping bentgrass) are common on golf course fairways north of the transition zone (1,16). Normally the creeping bentgrass is planted as the desired species and the annual bluegrass invades the bentgrass turf via annual bluegrass seed present in the soil or carried in by foot traffic or machinery (7,12). Annual bluegrass has many undesirable agronomic characteristics which makes its reliability as a perennial turf questionable. Annual bluegrass is susceptible to many pathogens and is physiologically weakened by high temperature (2,4,16).

Plant growth regulators have been proposed as a useful tool for conversion of turf polystands. Hubbel and Dunn (11) found mefluidide (N-[2,4-dimethyl-5 [[(trifluoromethyl) sulfonyl] amino] phenyl] acetamide), in combination with preplant nitrogen treatments, to enhance the spread of zoysiagrass (*Zoysia japonica* Steud.) transplanted into Kentucky bluegrass (*Poa pratensis* L.). Fry and Dernoedon (9) reported enhanced zoysiagrass spread into perennial ryegrass (*Lolium perenne* L.) treated with mefluidide or amidichlor (N-[(acetylamino) methyl]-2-chloro-N-(2,6-diethylphenyl) acetamide) and a slight increase in zoysiagrass spread into Kentucky bluegrass treated with mefluidide. Recently, PGR's have been studied for selective growth suppression of annual bluegrass. Breuninger and Watschke (4) found EL-500 (α -(1-methylethyl)- α -[4-trifluoro- methoxy)phenyl] 5-pyrimidene methanol) and the herbicide endothall (7-oxabicyclo[2,2,1] heptane-2,3-dicarboxylic acid) significantly reduced annual bluegrass in perennial rye, while mefluidide inhibited seedhead production but did not reduce annual bluegrass populations. Shearman (13) reported a reduction in annual bluegrass competition in cool season turf following late season mefluidide and EL-500 applications. Following EL-500 treatment of a mixed stand of annual bluegrass and creeping bentgrass, Shoop et al. (14) reported a visual decrease in annual bluegrass. These results suggest a potential for the use of EL-500 in the conversion of annual bluegrass/creeping bentgrass stands to creeping bentgrass, however quantitative data is lacking. The purpose of this research was to quantify the encroachment of creeping bentgrass into annual bluegrass following EL-500 treatment.

METHODS AND MATERIALS

Research was conducted at the Hancock Turfgrass Research Center, East Lansing, MI. on a mature stand of annual bluegrass maintained at 13 mm clipping height. The area was mowed three times/week with a triplex mower and clippings were returned to the turf. Fertility rate was 146 kg N ha^{-1}

yr^{-1} applied as urea. Irrigation and fungicides were applied as needed to prevent drought and disease. In April of 1985 cores of 'Penncross' creeping bentgrass with an area of 91 cm^2 were transplanted into the experimental area. Three cores were transplanted into plots 1.8 X 1.2 m. EL-500 treatments were applied with a hand held CO_2 sprayer calibrated to deliver 467 L ha^{-1} at 0.21 MPa. EL-500 rates and dates of application are shown in Table 9. Experimental design was a randomized complete block with 3 replications.

Table 9. EL-500 rates and dates of application for bentgrass encroachment study. Hancock Turfgrass Research Center. East Lansing, MI.

EL-500 Rate (kg ha^{-1})	Date of Application 1985	1986
1.68	5/14	4/29
1.68	8/15	8/20
1.12	5/14	4/29
1.12	8/15	8/20
0.56 + 0.28 + 0.28	5/14,5/31,6/17	4/29,5/13,5/30
0.56 + 0.28 + 0.28	8/15,8/30,9/15	8/20,9/6,9/21
0.56 + 0.56	5/14,5/31	4/29,5/13
0.56 + 0.56	8/15,8/30	8/20,9/6
1.12 + 1.12	5/14,8/15	4/29,8/20
CONTROL	---------	---------

Data were collected by measuring the area of the bentgrass cores in August and November of 1985 and July and October of 1986. Bentgrass area was measured by placing a piece of clear acetate film over the core and tracing the perimeter of the core with an indelible marker. The area of the trace was measured with a digital planimeter. An analysis of variance was computed for each measurement date to evaluate treatment differences.

RESULTS AND DISCUSSION

Results of the analysis of variance for treatments for all measurement dates were non-significant at the 0.05 level of probability. Although the F-test in the analysis of variance was non-significant, examination of treatment means (Table 10) shows some interesting trends. The area of the bentgrass cores, regardless of treatment, increased over time. Under golf course conditions annual bluegrass is normally more aggressive than creeping bentgrass, becoming

Table 10. Mean area of creeping bentgrass (*Agrostis palustris* Huds. cv. 'Penncross') cores in annual bluegrass (*Poa annua* (Hausskn.) Timm. var. *reptans*) following EL-500 treatment.

EL-500 Rate (kg ha^{-1})	Area 1985 Aug.	Nov.	1986 July	Oct.
	cm^2			
1.68 (Spring)	76	88	260	259
1.68 (Fall)	84	80	207	291
1.12 (Spring)	77	79	238	272
1.12 (Fall)	78	85	263	282
0.56 + 0.28 + 0.28 (Spring)	78	89	287	310
0.56 + 0.28 + 0.28 (Fall)	68	86	217	332
0.56 + 0.56 (Spring)	77	79	243	344
0.56 + 0.56 (Fall)	77	81	281	319
1.12(Fall) + 1.12 (Spring)	87	89	254	298
CONTROL	72	88	308	398
C.V. (%)	12.1	14.4	30.9	30.8

+ Mean area of 3 cores/plot with 3 replications (n = 9) established by seed and/or rapid tillering in voids left in the turf by mismanagement, wear and compaction, and disease and moisture stress (1,7,16). The low traffic, optimal moisture, and fungicide applications utilized in this study were not conducive to annual bluegrass encroachment. These data suggests that the creeping bentgrass, under the optimal growing conditions of this study, was more aggressive or competitive than the annual bluegrass.

The results of this study may have been influenced by mowing practices. When a PGR is applied to turfgrass a reduction in mowing frequency, based on reduced clipping yields, is usually observed (3,6). The experimental site in this study was mowed three times per week at 13 mm. This high mowing frequency may have suppressed the selective growth suppression reported by others (4,13,14). In addition, Field and Whitford (8) found mowing timing, either before or after treatment, was critical to mefluidide efficacy applied to perennial ryegrass. Although mefluidide is primarily foliar absorbed (8) and EL-500 is primarily root absorbed (ELANCO Products Co., 1983, personal communication) mowing frequency and timing may affect the efficacy of EL-500.

In previous studies (4,14) changes in annual bluegrass populations were estimated visually. The color enhancement which follows EL-500 applications (5,10) may mask the yellowish or light green color normally exhibited by annual bluegrass, causing an evaluator to perceieve a decrease in annual bluegrass, although this has not occurred.

The data in Table 10 suggest that, over time, EL-500 treatments impaired the encroachment of creeping bentgrass, when compared to the control. EL-500 has been shown to slow the establishment of zoysiagrass in Kentucky bluegrass and perennial ryegrass (9). The data, for the October 1986 evaluation, exhibits a trend for single applications of EL-500 at 1.68 and 1.12 kg ha^{-1} to suppress the spread of creeping bentgrass more than split applications of EL-500 at 1.12 kg ha^{-1}

At the rates and timings tested, EL-500 was ineffective in enhancing the encroachment of creeping bentgrass into annual bluegrass. Mowing practices utilized may have reduced the efficacy of the EL-500. The effects of mowing frequency and timing on the efficacy of PGR's applied to turf warrents furthur investigation.

REFERENCES

1) Beard, J.B. 1973. Turfgrass:Science and culture. Prentice Hall, Inc., Englewood Cliffs, N.J. 658 pp.

2) 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.

3) Brauen, S., D. Frye, B. Osborne, and R. Goss. 1983. Maintenance mowing reduction and turfgrass response to growth regulants. p. 130-141 *In* Proc. 37th Annual Meeting Northwest Turf Conf. Warm Springs, OR. 19-22, Sept. 1983.

4) Breuninger, J.M.and T.L. Watschke. 1982. Post emergent Poa annua control with growth retardents. p.314. *In* Proc. 36th Meeting Northeastern Weed Sci. Soc. New York, NY. 5-7, Jan. 1982. Evans Printing, Inc. Salisbury, MD.

5) Breuninger, J.M., T.L. Watschke, and L.D. Tukey. 1983. Effect of PP-333 and flurprimidol (EL-500) on tall fescue in an apple orchard. p. 370. *In* Proc. 37th Meeting Northeastern Weed Sci. Soc. Grossinger, NY. 4-6, Jan. 1983. Evans-Coates Printing, Inc. Salisbury, MD.

6) Christians, N.E. 1985. Response of Kentucky bluegrass to four growth retardents. J. Amer. Soc. Hort. Sci. 110:765-769

7) Engel, R.E. and R.D. Ilnicki. 1969. Turf weeds and their control. In A.A. Hanson and F.V. Juska (ed.) Turfgrass Science. Agronomy 14:240-287.

8) Field, R.J. and A.R. Whitford. 1982. Effect of simulated mowing on the translocation of mefluidide in perennial ryegrass (*Lolium perenne* L.). Weed Research. 22:177-181

9) Fry, J.D. and P.H. Dernoedon.1986. Zoysiagrass competition in two cool-season turfgrasses treated with plant growth regulators. Hort Sci. 21:464-466.

10)Gaussoin, R.E., B.E. Branham, and P.E. Rieke. 1985. Cultural factors in annual bluegrass and creeping bentgrass competition. p. 35-37. *In* Proc. 55th Annual Mich. Turfgrass Conf. Lansing, MI 21-23, Jan. 1985. Mich. Turf Found., Mich Ag. Expt. Sta. and Coop. Ext. Service, Michigan State Univ. East Lansing, MI.

11)Hubbel, G.P. and J.H. Dunn. 1985. Zoysiagrass establishment in Kentucky bluegrass using growth retardents. J. Amer. Soc. Hort. Sci. 110:58-61.

12)Jagshitz, J.A. 1986. Establishment of turfgrass, crabgrass and annual bluegrass following herbicide use. p. 270-271. *In* Proc. 40th Annual Meeting Northeastern Weed Sci. Soc. Boston, MA. 7-9, Jan. 1986. Evans-Coates Printing, Inc. Salisbury, MD.

13)Shearman, Robert. 1986. Weed control guide:Cool season turf. Weeds, Trees and Turf. 23:76,80.

14)Shoop, G.L., R.H. Hoefer and D.G. Ortega. 1986. Flurprimidol (EL-500) growth regulator effect on bentgrass fairways in the northeast. p. 131. *In* Proc. 40th Annual Meeting Northeastern Weed Sci. Soc. Boston, MA. 7-9, Jan. 1986. Evans-Coates Printing, Inc. Salisbury, MD.

15)Watschke, T.L. and J.M. Duich. 1977. Control of *Poa annua* with endothal. p. 357-359 *In* Proc. 31st Meeting Northeastern Weed Sci. Soc. Baltimore, MD. 4-6, Jan. 1977. Evans Printing, Inc. Salisbury, MD.

16)Wilson, C.G. and J.M. Latham, Jr. 1969. Golf fairways, tees and roughs.In A.A. Hanson and F.V.Juska (ed.) Turfgrass Science. Agronomy 14:584-602.

Reprinted from HortScience, Vol. 22(3), June 1987
A publication of the American Society for Horticultural Science, Alexandria, Virginia

HortScience 22(3):441–442. 1987.

Annual Bluegrass and Creeping Bentgrass Germination Response to Flurprimidol

R.E. Gaussoin[1] **and B.E. Branham**[2]
Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824

Additional index words. *Poa annua*, *Agrostis palustris*, flurprimidol

Abstract. **Seed of *Poa annua* var. *reptans* (Hauskins) Timm. (annual bluegrass) and *Agrostis palustris* Huds. 'Penncross' (creeping bentgrass) were treated at planting with flurprimidol at rates of 0.00, 0.28, 0.56, 0.84, 1.12, 1.68, and 2.24 kg·ha^{-1}. Data were collected on germination of each species. Flurprimidol rates greater than 0.56 decreased germination for both species. Chemical name used: α-(1-methylethyl-α-[4-(trifluoromethoxy)phenyl]-5-pyrimidine methanol (flurprimidol).**

Poa annua L. (annual bluegrass) invades close-cut, irrigated, intensively managed cool season turfs and within 3 to 5 years may dominate the stand (11). Annual bluegrass may invade desired species, filling voids left by mismanagement, disease, traffic, cultivation, and other stresses (1). Annual bluegrass may reestablish these areas vegetatively (1) or from seed in the soil (7). Control programs are based on the removal of annual bluegrass over a number of years while managing the turf for the desired species, or reestablishment of the desired species after annual bluegrass eradication (2, 5, 8). One management approach would be to employ a plant growth regulator to inhibit selectively the growth of annual bluegrass and encourage the desired species, allowing a gradual transition from annual bluegrass dominance while maintaining turfgrass aesthetic and functional qualities. Flurprimidol reduced annual bluegrass in perennial ryegrass (*Lolium perenne* L.) (2). Flurprimidol applied to annual bluegrass and creeping bentgrass (*Agrostis palustris* Huds.) polystands exhibits selectivity for annual bluegrass growth suppression, indicating a potential for use in the conversion process (10). If the annual bluegrass population in a mixed stand is very high, overseeding with creeping bentgrass is sometimes implemented. Haley and Fermanian (6) found that flurprimidol was active on young seedlings of annual bluegrass and creeping bentgrass, but information on germination response was not reported. The objective of this research was to determine if flurprimidol applications influenced germination of annual bluegrass and creeping bentgrass.

Clay pots 100 mm in diameter were seeded in the greenhouse, where temperatures fluctuated between 10° and 24°C. The growth medium was 5 sandy loam : 3 sand : 1 peatmoss, (by volume). Half the pots were seeded to 'Penncross' creeping bentgrass (lab germination 85%). The remaining pots were seeded to annual bluegrass (lab germination 92%). Both species were seeded at a rate of 25 seeds/pot. Seed of annual bluegrass was obtained by harvesting mature seed heads from a stand of annual bluegrass located at the Hancock Turfgrass Research Center, Michigan State Univ. The harvested seed was assumed to be of the perennial annual bluegrass biotype, due to the high germination (92%) observed immediately after harvest (1).

Immediately following seeding, pots were treated with flurprimidol at rates of 0.00, 0.28, 0.56, 0.84, 1.12, 1.68, and 2.24 kg·ha^{-1}. Treatments were applied with a backpack CO_2 sprayer with an 8002E nozzle calibrated to deliver 384 liters·ha^{-1}. Pots were irrigated three times daily for 4 min with an automatic misting system. The experiment was conducted on two dates (Oct. 1984 and

---

Received for publication 6 Oct. 1986. Contribution from the Michigan Agricultural Experiment Station Journal Article 12104. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

[1] Graduate student.

[2] Assistant Professor.

Table 1. Flurprimidol effects on annual bluegrass (*Poa annua* var. *reptans*) and creeping bentgrass (*Agrostis palustris* 'Penncross') germination. Values presented represent means of both species.

	Germination (%)[z]	
Rate (kg·ha^{-1})	Test date 1	Test date 2
0.00	100	100
0.28	92.0	92.3
0.56	86.7	85.3
0.84	86.7	78.3
1.12	81.0	76.3
1.68	47.7	60.0
2.24	50.3	73.7

[z] Percent germination for the controls were normalized and treatment values were adjusted to a percentage of the control. Germination counts taken 21 days after treatment.

LSD (P = 0.05) for test date = 6.5%; LSD (P = 0.05) for rate = 8.4%.

Jan. 1985). Data were collected on the number of seed germinating per pot. Nongerminating seed were examined for evidence of radicle emergence. Pots were arranged in a randomized complete block. The rate and species factors were split on the date of test factor for a 2 × 7 × 2 factorial treatment design. On each test date, six replications were used. Mean separation was accomplished using the least significant difference (LSD) multiple comparison technique.

Results of the analysis of variance showed that flurprimidol rates and date of test were significant sources of variation. A significant rate × test date interaction also was observed; however, no variability due to species was observed. As flurprimidol rate increased, germination generally decreased. Rates ≥ 0.56 kg·ha^{-1} significantly reduced germination when compared to the control (Table 1). The significant rate × test date interaction and test date main effect result from the germination values observed for the 1.68 and 2.24 kg·ha^{-1} rates. No explanation is evident for the significant rise in germination observed for the 2.24 kg·ha^{-1} rate in test date 2.

Examination of nongerminating seed found no evidence of radicle emergence, indicating that flurprimidol may act as a germination inhibitor. Flurprimidol is in a class of plant growth regulators shown to inhibit gibberellic acid (GA) biosynthesis (3, 4). Gibberellic acid is produced in the embryo of the grass seed during germination. The GA produced stimulates the cells of the aleurone layer to manufacture α-amylase, an enzyme necessary for endosperm digestion (9). If the embryonic production of GA is inhibited by flurprimidol, the products normally made available from endosperm digestion are limited, which may account for the germination inhibition seen in this study.

Results of this experiment indicate that at low rates (0.28 kg·ha^{-1}), flurprimidol exhibits no inhibition of annual bluegrass or creeping bentgrass germination. At rates ≥ 0.56 kg·ha^{-1}, both species show the same germination response to flurprimidol application. Thus, there would be no advantage in using flurprimidol in an overseeding program in terms of reducing the competition from germinating annual bluegrass. Results also indicated that the use of flurprimidol at rates ≥ 0.56 kg·ha^{-1} should not be practiced at or near time of bentgrass overseeding. If overseeding is not planned, flurprimidol will have some preemergence activity on annual bluegrass seed present in the soil. Only one biotype of annual bluegrass was evaluated, and the extreme variability exhibited by this species should be considered when extending these results to all annual bluegrass biotypes.

Literature Cited

1. Beard, J.B., P.E. Rieke, A.J. Turgeon, and J.M. Vargas. 1978. Annual bluegrass (*Poa annua* L.) description, adaptation, culture and control. Michigan State Univ. Agr. Expt. Sta. Res. Rpt. 352.
2. Breuninger, J.M. and T.L. Watschke. 1982. Post emergent *Poa annua* control with growth retardents. Proc. Northeastern Weed Sci. Soc. 36:314.
3. Coolbaugh, R.C., S.S. Hirano, and C.A. West. 1978. Studies on the specificity and site of action of α-cyclopropyl-α-[p-methoxyphenyl]-5-pyrimidine methyl alcohol (ancymidol), a plant growth regulator. Plant Physiol. 62:571–576.
4. Coolbaugh, R.C., D.I. Swanson, and C.A. West. 1982. Comparative effects of ancymidol and its analogs on growth of peas and *ent*-kaurene oxidation in cell free extracts of immature *Marah mucrocarpus* endosperm. Plant Physiol. 69:707–711.
5. Engel, R.E. and R.J. Aldrich. 1960. Reduction of annual bluegrass, *Poa annua*, in bentgrass turf by the use of chemicals. Weeds 8:26–28.
6. Haley, J.E. and T.W. Fermanian. 1985. The effect of flurprimidol on germination and development of *Poa annua* and *Agrostis palustris*. Agron. Abstr. p. 116.
7. Jagshitz, J.A. 1986. Establishment of turfgrass, crabgrass, and annual bluegrass following herbicide use. Proc. Northeastern Weed Sci. Soc. 40:270–271.
8. Jagshitz, J.A. 1979. Annual bluegrass control in Kentucky bluegrass turf with herbicides. Proc. Northeastern Weed Sci. Soc. 33:308–313.
9. Salisbury, F.B. and C.W. Ross. 1978. Plant physiology. Belmont, Calif. Wadsworth, 2nd Edition.
10. Shoop, G.J., R.H. Hoefer, and D.G. Ortega. 1986. Flurprimidol (EL-500) growth regulator effect on bentgrass fairways in the northeast. Proc. Northeastern Weed Sci. Soc. 40:131.
11. Watschke, T.L. and J.M. Duich. 1977. Control of *Poa annua* with endothal. Proc. Northeastern Weed Sci. Soc. 31:357–360.

TURFGRASS PHOTOSYNTHESIS: A REVIEW

Photosynthesis is the only significant process through which non-nutritious inorganic compounds are converted into essential foodstuffs for plants. The plants then become available for human and animal consumption and in the case of turfgrasses, recreation. An understanding of photosynthesis and conditions which control it are important in all plant science disciplines and a review of the literature is essential in gaining this understanding. The intent of this paper is to review the literature for photosynthetic research pertaining to turfgrass species and cultural practices. This review is primarily confined to scientific journal articles and will contains literature which refers to grass species used both in turfgrass and forage management.

ENVIRONMENTAL EFFECTS

Light. Cooper and Wilson (13) reported photosynthetic saturation at 20,000-30,000 lux for annual (*Lolium multiflorum* Lam.) and perennial (*L. perenne* L.) ryegrass. Photosynthetic saturation for creeping bentgrass *(Agrostis palustris* Huds. or *A. stolonifera* var. *palustris* (Farwell)) has been reported to be about 500μmol m^{-2} s^{-1} (53).

Alexander and McCloud (3) reported maximum photosynthesis for isolated leaves of bermudagrass (*Cynodon dactylon* (L). Pers.) at 2500 to 3000 foot-candles, with a light compensation point of 300 foot-candles. Growth of red fescue (*Festuca rubra* L.) and Kentucky bluegrass (*Poa pratensis* L.) at low light intensities resulted in a low carbon dioxide exchange rate (CER), when measured at saturating or growth-condition light levels (71). Winstead and Ward (74) studied the CER of warm season turfgrasses in shade and found bermudagrass to display a decrease in CER under shade while St. Augustinegrass (*Stenotaphrum secundatum* (Walt.) Kuntze) showed a slight increase. Morgan and Brown (46) investigated light response in Coastal bermudagrass and reported the response of CER to photosynthetic photo flux density (PPFD) followed a rectangular hyperbola with the curves becoming more linear and maximum CER increasing as leaf area index (LAI) increased. It has been shown that saturation (i. e. maximum photosynthesis) requires greater levels of ambient light under simulated swards than that required for saturation of individual bermudagrass leaves and that swards with a height of eight and 14 inches (before mowing) required a lower ambient light level for saturation than swards at 20 and 26 inches (3). Dienum (16) demonstrated that shading and defoliation of the axillary tillers of vegetative annual ryegrass plants stimulated leaf photosynthesis of the main shoot which coincided with a lower stomatal and internal diffusive resistance and lower soluble carbohydrate content, suggesting that the stressed tillers function as sinks for the assimilates. Woledge (77) showed that as the leaf area of swards of perennial ryegrass increased, successive leaves which expanded on the main stem of the sample plant within the sward had progressively lower photosynthetic capacities, postulated to be due to the newer leaves expanding under lower illumination levels. Further work by Woledge (76) showed that this decline in photosynthesis could be prevented by protecting tillers from shading during growth. Woledge (75) measured higher photosynthesis in the leaves of reproductive tillers and concluded that this increase was because stem extension carries these leaves to the top of the canopy where they are well illuminated during expansion. Meadow fescue (*Festuca pratensis* Huds.) when grown at two light intensities had higher CER in plants preconditioned at the higher light intensity (42).

Temperature. Miller (44) measured the rate of apparent photosynthesis in Seaside creeping bentgrass and Common bermudagrass at six temperatures. The relative rate of photosynthesis for creeping bentgrass increased from 65% at 15 °C to a maximum of 100% at 25°, than decreased to 62% at 40 °C. The relative rate for bermudagrass increased from 55% at 15 °C to a maximum of 100% at 35° and dropped to only 98% of maximum at 40 °C. Schmidt and Blaser (61) reported a 172% increase in net photosynthesis in Tifgreen bermudagrass (*Cynodon dactylon* X *C. transvaalensis*) when measured at 24

°C vs. 12 °C and a 96% increase when measured at 24 °C vs. 36 °C. Watschke et al. (69) found that growth for three weeks at 35 °C reduced the net photosynthesis of eight cool season turfgrass cultivars, when compared to growth at 23 °C. Rogers et al. (57) reported no significant differences in CER, based on unit land area, between three *Zoysia* spp. and three bermudagrass cultivars when measured during cold hardening. Woledge and Parsons (81) showed that as ambient temperature increased from 10 to 25 °C canopy photosynthesis in a sward of perennial ryegrass increased. Woledge and Dennis (78) found that growth temperature had little effect on the rate of leaf photosynthesis in perennial ryegrass, but measurement temperature strongly influenced assimilation, with rates measured at 15 °C being twice those at 5 °C. A similar response has been shown in tall fescue (*Festuca arundinacea* Schreb.) (79). Pammentor (53) reported the optimal temperature range for CER in creeping bentgrass to be between 15 and 25 °C. Schmidt and Blaser (62) measured the net photosynthesis of Cohensey bentgrass at three temperatures and found that 80% more CO_2 was fixed at 24 vs. 12 or 36 °C. Duff and Beard (20) found that preconditioning creeping bentgrass at supraoptimal temperatures increased photosynthesis. Plants preconditioned at 30-40 °C had significantly higher photosynthetic rates than plants at 25-35, 20-30, or 15-25 °C. The lowest photosynthetic rate was in plants preconditioned at 10-20 °C. All plants were measured at the highest range of their growth temperature. When plants grown at 10-20 or 30-40 °C were measured at temperatures of 20, 30 and 40 °C, the plants preconditioned at the higher temperature exhibited a higher photosynthetic rate at all three test temperatures. Davidson and Robson (15) found no difference in canopy photosynthetic rate (g CO_2 m^{-2} h^{-1}) for perennial ryegrass plants preconditioned and measured at either high (20 °C day/15 °C night) or low (10 °C day/8 °C night) temperature. Labhart et al. (42) found preconditioning temperature to have no effect on CER in meadow fescue. Murata and Iyama (48) found maximum photosynthesis for annual and perennial ryegrass to occur around 10 °C, with a steep decline after 25 °C, while bermudagrass and bahaigrass (*Paspalum notatum* Flugge.) had photosynthetic maximums near 35 °C. Ollerenshaw et al. (50) found a cold adapted selection of red fescue to have a higher photosynthetic rate than a less cold adapted selection, when assimilation was measured at 2 °C. The CER of two bermudagrass cultivars (Ormond and Pee Dee) and two St. Augustinegras cultivars (Texas Common and Floratam) was monitored continuously for 14 days at chilling temperatures (day/night, 7/5 °C, respectively) by Karnok and Beard (35). Ormond, Pee Dee, Texas Common, and Floratam showed reductions of 54, 68, 79, and 84%, respectively, in daytime CER during the initial chilling period.

Carbon Dioxide. Krenzer and Moss (39) measured the CO_2 compensation points for 325 species of Graminaea. In

general species in the *Festucoideae* subfamily had high compensation points and those in the subfamily *Panicoideae* low compensation values. The CO_2 compensation points for nineteen species of Graminaea was measured by Downton and Tregunna (19) with all C_4 species having low (<5 ppm) and C_3 species having high (37-50 ppm) compensation points. However, bermudagrass (compensation point 5 ppm) was the only turf species evaluated. Imai et al. (31) found zoysiagrass (*Zoysia japonica* Steud.)to have a CO_2 compensation point of 1 ppm. Brown and Brown (6) reported a CO_2 compensation point of 54 ppm for tall fescue. Watschke et al. (69) found that preconditioning eight cool season turfgrass cultivars at 35 vs. 23 °C increased the CO_2 compensation point, while preconditioning temperature did not effect the compensation point of bermudagrass. Beard (5) reported that the microclimate under shade trees is higher in CO_2 than an unshaded area, which may affect photosynthesis.

Diurnal/Daylength. The effect of daylength on photosynthesis in annual bluegrass (*Poa annua* L.) and rough bluegrass (*Poa trivialis* L.)was investigated by Burian and Winter (9). Although short day conditions (8 h/16 h) decreased net production, the photosynthetic rate of short day grown plants was nearly twice as much as plants grown in long day (16 h/ 8 h) conditions. Application of red light early or in the middle of the dark period further increased the photosynthetic rate of short day plants and decreased

the rate in long day plants. Far-red light applied in the middle of the dark period produced the opposite effect. The authors concluded that the effect of red and far-red irradiation on chlorophyll synthesis did not sufficiently explain the apparent phytochrome dependent control of photosynthesis. Hay and Heide (27) reported that Kentucky bluegrass plants raised under short days gave significant increases in dry weight upon exposure to continuous light, compared with 8-h short days, at essentially identical daily inputs of radiant energy. This increase in relative growth rate was postulated to be due primarily to increased net assimilation rate followed, several days later, by increases in leaf area ratio when newly-emerged leaves began to constitute a significant portion of the leaf area. Murata and Iyama (47) found annual ryegrass to exhibit diurnal fluctuations in apparent photosynthesis. The fluctuations, however, coincided very closely to ambient CO_2 concentrations. Hansen (26) found root respiration in perennial ryegrass to exhibit diurnal fluctuations, with two characteristic peaks occurring 4-6 and 14-16 h after onset of the photoperiod, and respiration was dependent on net assimilation. Hull (30) measured diurnal variation in assimilate partitioning in Kentucky bluegrass and found that assimilate translocation from leaves to stems was more rapid in the morning than the afternoon, and translocation to roots was greater after noon. Rhizomes received little

photosynthate within the measurement period and exhibited no diurnal pattern.

Oxygen Inhibition. Brown and Brown (6) reported that an O_2 concentration of 21% reduced the net photosynthesis of tall fescue 40% when compared to an O_2 free environment. Downes and Hesketh (18) tested nearly 50 grass species for enhancement of photosynthesis in a low ($< 1\%$) O_2 environment. All turfgrass species evaluated were C_3 types and included Kentucky bluegrass, annual ryegrass, and two *Agrostis* spp., with all showing significantly higher photosynthetic rates at the low O_2 condition. Watschke et al. found that the photosynthesis of cool season species approached that of bermudagrass when photorespiration was inhibited by low O_2 concentration (69), and that in 10 strains of Kentucky bluegrass low O_2 concentrations resulted in nearly a two-fold increase in net assimilation (70). Glacoleva and Zalensky (22) showed that in bermudagrass photosynthesis was higher at 21% vs. 1% O_2.

Post Illumination CO_2 Burst (PIB). The evolution of CO_2 upon the transition of leaves from light to darkness was studied in 44 grass species by Brown and Gracen (7). Turfgrass species tested which exhibited the PIB were bermudagrass and tall fescue, while St. Augustinegrass and bahaigrass did not exhibit the PIB.

Atmosphere. Cowling and Koziol (14) found perennial ryegrass exposed to two levels of SO_2 (50 and 400 $\mu g\ m^{-3}$) to show visible injury symptoms, but no significant decrease in

net photosynthesis was observed. However, Beard (5) reported that the destruction of chlorophyll by SO_2 results in the inhibition of photosynthesis. Ho and Trappe (28) reported that the intensity of mycorrhiza formation in forage grasses relates directly to photosynthetic activity or assimilate availability, and when tall fescue was exposed to 0.1 ppm ozone for 3 months the reduction in the intensity of mycorrhiza formation was possibly caused by reduced photosynthesis in the host.

Wind. Grace and Thompson (23) found tall fescue plants subjected to simulated wind conditions in a controlled environment wind tunnel to have reduced rates of photosynthesis, higher mesophyll resistance and lower leaf surface resistance than control plants. The high mesophyll resistance in the wind-treated plant was attributed to reduced water content. However, Russel and Grace (59) found no difference in the gross photosynthesis of tall fescue or perennial ryegrass when subjected to wind speeds of 7.4 m s^{-1} or 1.0 m s^{-1}.

CULTURAL EFFECTS

Mineral Nutrition. Hull (29) reported that a Merion Kentucky bluegrass turf fixed more $^{14}CO_2$ at high fertility rates (24-4-8 or 48-8-16 g m^{-2} N-P-K) than at low fertility (12-2-4 g m^{-2} N-P-K). Davidson and Robson (15) found perennial ryegrass plants grown in a solution culture high in N (220 $\mu g\ g^{-1}$) to have canopy photosynthetic rates (g CO_2 m^{-2} h^{-1}) 30% higher than plants grown in low N (40 $\mu g\ g^{-1}$).

Tall fescue and creeping bentgrass, under growth conditions in Virginia, showed increased photosynthesis, on a plot area basis, for high N treatments (55). High N fertility levels have been shown to increase net photosynthesis, on a dry weight basis, for Tifgreen bermudagrass (61) and Cohansey bentgrass (62). In centipedegrass (*Eremochloa ophiuroides* (Munro.) Hack.) Walker and Ward (68) found increasing N fertility to increase CER on a leaf area basis, while increasing K fertility decreased CER. Robson and Parsons (56) found an increase in the photosynthetic rate, on both a leaf area and canopy basis, of perennial ryegrass at high N fertility levels. A comparison of the observed rates of canopy photosynthesis with those predicted by a mathematical model of canopy photosynthesis indicated that it was the effect of N on single leaf photosynthesis, rather than differences between the communities in leaf area which led to the observed differences in photosynthesis. Ruetz (58) found fertilized red fescue to have higher CER (leaf dry weight or leaf area basis) than unfertilized and that during the growing season the unfertilized plants had a continual decline in CER. Mehall et al. (43) found no relationship between CER and Kentucky bluegrass tissue K or P concentrations. In a growth chamber simulation of a late summer through mid fall Virginia growth cycle, Schmidt and Snyder (63) found applications of FeDTPA to decrease net photosynthesis of Penncross creeping bentgrass. Hull (30) found that diurnal photosynthate partitioning was

independent of fertility level in Kentucky bluegrass. However, translocation of assimilates from leaves to stems was faster in heavily fertilized turf (48-8-16 g m^{-2} N-P-K) while roots received more photosynthate in low fertility (12-2-4 g m^{-2} N-P-K) turf. Fertility influences were most evident during midsummer when roots and rhizomes constituted stronger sinks for assimilates.

Mowing/Clipping. Krans and Beard (37) reported that rates of apparent photosynthesis based on unit leaf area were higher in Merion Kentucky bluegrass plants clipped semiweekly than biweekly, but when based on total leaf area per pot this response was reversed. Youngner et al. (83) attributed the greater tolerance to mowing of Merion Kentucky bluegrass to higher leaf sheath CER in this variety. Ollerenshaw and Incoll (49) found that the photosynthetic rates of leaves of annual and perennial ryegrass were higher in swards cut constantly at 3 cm when compared to plants clipped at 9 cm and that the photosynthetic rate of annual ryegrass was higher than perennial ryegrass soon after mowing but the perennial ryegrass leaves quickly adapted to the higher irradiances received after clipping. In forage bermudagrass Morgan and Brown (46) found much lower CER for stands clipped weekly compared to plots mowed monthly, which was attributed to to the lower LAI in the weekly mowed plots. Alexander and McCloud (3) found severe clipping treatments, where large amounts of leaf and stem tissue were removed, to significantly reduce photosynthesis (on a leaf area basis) in bermudagrass and attributed the reduction to lack of leaf greenage in the stubble after clipping. Hart and Lee (25) reported that the much higher rate of NCE in younger leaves may explain the high production of frequently cut Coastal bermudagrass stands. As was reported in the Light section of this paper Dienum (16) demonstrated that defoliation and shading of the axillary tillers of vegetative annual and ryegrass plants stimulated leaf photosynthesis of the main shoot. Gifford and Marshall (21) reported that CER of the main shoot leaves of annual ryegrass were 15% greater the day after tiller defoliation than just before defoliation, which was attributed to a measured lower gas-phase resistance in the defoliated plants. Clark et al. (11) found that the photosynthetic rate of excised annual ryegrass leaves began to decline rapidly 1-2 min. after excision with two breaks of slope at 15 and 30 min. Examination of stomata found complete optical closure at 15 min. after excision.

Chemical. Kaufmann and Williamson (36) tested several chemicals to manipulate water consumption in Merion Kentucky bluegrass and measured the effect of these chemicals on photosynthesis. The wetting agent Hydrowet and the fungicide benomyl (Methyl-1-(butylcarbamoyl)-2-benzimidazole-carbamate) significantly reduced CER while Aquagro (wetting agent) and the fungicide iprodione (3-(3,5-Dichlorophenyl)-N-(1-methylethyl)-2,4-dioxo-1-

imidazolidinecarboxamide) did not affect photosynthesis. DeMur et al. (17) reported that siduron (1-(2 methylcyclohexyl)-3-phenylurea) inhibited electron transport in isolated chloroplasts of bermudagrass and Kentucky bluegrass with the site of inhibition in photosystem II between water splitting and photosystem I. Moss (45) found a high correlation between grasses with a high photosynthetic activity and atrazine tolerance. Bromacil (5-bromo-3-*sec*-butyl-6-methyluracil) has been shown to inhibit photosynthesis in Kentucky bluegrass (65,66). Yang and Bingham (82) found metribuzin (4-amino-6-*tert*-butyl-3-(methylthio)-*as*-triazin-5(4*H*)-one) to inhibit the CO_2 uptake of six cultivars of bermudagrass, but full photosynthetic rate was recovered within 24 h after treatment for low metribuzin rates and several days after treatment for high metribuzin rates. Karnok and Beard (35) found exogenous applications of gibberellic acid to increase the daytime CER of two cultivars of bermudagrass (Ormond and Pee Dee) and decrease daytime CER in Floratam St. Augustinegrass, after growth at chilling temperatures.

Irrigation/Water Stress. Schmidt and Snyder (63) found net photosynthesis to decline with decreasing moisture levels in Penncross creeping bentgrass. Asay et al. (4) reported rates of net photosynthesis in tall fescue to be significantly higher under irrigated vs. non-irrigated conditions. Brown and Simmons (8) subjected the roots of tall fescue to drying conditions to induce water stress and reported a decrease in net photosynthesis which was associated with decreases in stomatal plus boundary layer conductance and mesophyll conductance. Agnew and Carrow (1) found that after a water stress irrigation treatment (irrigation at -0.400 MPa for 99 days) stomatal diffusive resistance (R_s) increased in Kentucky bluegrass and concluded that this increase in R_s would decrease photosynthetic rate. Woledge and Parsons (81) reported a decrease in gross canopy photosynthesis in perennial ryegrass when measured at low humidity. Wilson (72) found perennial ryegrass selection lines with high calculated R_s maintained leaf photosynthetic rates longer than selection lines with low R_s when deprived of water. Jones et al. (33) reported that, after water stress, the canopy photosynthesis of both simulated and field-grown perennial ryegrass was significantly reduced. In the field grown plants the reduction was partially due to a lower leaf area but the rate of leaf photosynthesis (P_{max} / LAI) was reduced by about 40% which was attributed to a measured increase in stomatal resistance. In perennial ryegrass, Sheehy et al. (64) found an increase in leaf resistance to gas exchange with increasing moisture stress, with a corresponding increase in CO_2 compensation point and a decrease in leaf and canopy photosynthesis. Peacock and Dudeck (54) investigated the effect of irrigation scheduling on the CER of St. Augustinegrass and found that irrigation at 6 day

intervals reduced the CER prior to irrigation, but the CER returned to normal levels soon after irrigation.

Compaction. Agnew and Carrow (1) reported that long term compaction (compaction treatments equivalent to 720 J energy over a 99-day period) increased R_s in Kentucky bluegrass and concluded that higher R_s would result in lower photosynthesis. On zoysiagrass in Japan, Akiyama and Kubo (2) reported a maximum depression in photosynthesis four days after application of compression treatments (0.00, 2.50, 3.75, and 5.00 kg cm^{-2}) but the plants compressed at 2.5 kg cm^{-2} recovered their photosynthetic rate comparable to control plants within 3 weeks after compression, while the plants compressed to 5.00 kg cm^{-2} recovered 70% of the control plot photosynthesis within three weeks.

PHYSIOLOGICAL, MORPHOLOGICAL and GENETIC EFFECTS

Genetics. Watschke et al. (70) measured significantly different rates of CER among ten strains of Kentucky bluegrass, but the strains did not differ in their CO_2 compensation points. Asay et al. (4) reported significant differences for net carbon exchange (NCE) among tall fescue clonal lines and their polycross progenies under sward conditions in the field, with heritability estimates from 0.57-0.83, indicating that genetic progress could be made through selection for NCE rate in tall fescue. Cohen et al. (12) also found genetic variability among tall fescue for NCE with low yielding selections exhibiting significantly higher NCE than higher yielding selections. The authors concluded that single-leaf NCE is a necessary component of forage yield, but is apparently not a major component for yield determination. Youngner et al. (83) showed significant differences between Merion (higher CER) and Newport Kentucky bluegrass for net assimilation on a whole plant basis but not when expressed on an individual leaf basis. The higher rate for Merion was attributed to a higher rate of CER for the leaf sheath in Merion. Joseph et al. (34) found that net photosynthesis on a leaf area and leaf weight basis increased significantly with ploidy in a 4X, 6X, 8X, and 10X allopolyploid series of tall fescue. Krueger and Miles (40) found the electron transport activity for Photosystem I to be higher in a decaploid tall fescue as compared to a common hexaploid genotype. The decaploid genotype also exhibited a higher photosystem whole chain (Photosystem II plus Photosystem I uncoupled) activity, suggesting a connection between polyploidy and increased electron transport activity. Cooper and Wilson (13) found populations and genotypes of annual and perennial ryegrass to differ in their photosynthetic rate at both high and low light intensity with roughly equal heritabilities under both conditions. The data suggested that effective response to selection should be possible for both light-saturated and light-limited photosynthesis.

Leaf Age/Position. Hart and Lee (24) found the NCE of bermudagrass leaves to be highest at collar emergence and decrease with age. Jewiss and Woledge (32) found the apparent photosynthesis of tall fescue leaves to decline in a curvi-linear fashion when measured from full expansion to leaf death. Woledge and Leafe (80) found that canopy photosynthesis of perennial ryegrass declined due to leaf age when no further leaves were produced after flowering. The dry weight of the leaf did not change as it aged and net photosynthesis results were similar when expressed on either a leaf area or dry weight basis. Photosynthesis in leaves of bahiagrass is relatively stable from emergence to 30 days after emergence, than exhibits a severe decline starting 45 days after emergence (60). Krans and Beard (38) measured the net photosynthesis of seedlings of Kentucky bluegrass and red fescue from seedling emergence to 10 weeks after emergence. Net photosynthesis was greatest one week after emergence for both species. Wilson and Cooper (73) found apparent photosynthesis in fully expanded perennial ryegrass leaves to be higher in in the lower (older) leaves than in the upper (younger) leaves and for any particular leaf, maximum photosynthesis was attained prior to full expansion. Silcock and Wilson (67) measured photosynthesis in fescues which differed in leaf orientation and reported differences in the photosynthesis/ transpiration ratio based on leaf orientation.

Electron Transport. Chen et al. (10) measured the photosynthetic activity of isolated chloroplasts of bermudagrass and concluded that the high activity of bermudagrass could be supported by the photophosphorylation

capacities measured in these chloroplast studies. As was discussed in the Genetics section Krueger and Miles (40) suggested a connection between ploidy and increased electron transport activity. In further studies on electron transport in decaploid tall fescue Krueger et al. (41) found the decaploid tall fescue to have a higher plastocyanin content than the hexaploid type. Isolated thylakoid antibodies did not inhibit electron transport (diaminodiurene to methyl viologen) strengthening the hypothesis of plastocyanin as an internal electron shuttle.

Inflorescence Assimilation. The inflorescence of annual bluegrass has been shown to be an important assimilatory organ after grain ripening when it exports more than 50% of its assimilate to the stem, roots and other tillers (52). Ong et al. (51) investigated the assimilation of $^{14}CO_2$ by the infloresence of annual bluegrass and perennial ryegrass determined from inflorescence emergence to seed shedding. Both species exhibited the same fixation pattern, with the infloresence being the greatest assimilatory organ on the reproductive tiller. Except for the seeds all parts of the inflorescence showed significant assimilatory activity with the lemma and palea accounting for 40-50% of ^{14}C fixed.

Feedback Inhibition. In annual ryegrass Hansen (25) found that on the first day of a period of high irradiance, CO_2 assimilation was higher on a leaf area basis than on the following day day of high irradiance, and an accumulation of storage material took place. On the first day of a period

of low irradiance, the assimilation was lower than on the following a day of low irradiance, and there was a depletion in stored assimilates. These effects were most evident during a regrowth period, indicating a change in metabolic sink demand. Hansen (25) proposed that a strong feedback mechanism between sources and sinks exists, in the sense that accumulation of products will inhibit assimilation.

REFERENCES

1) Agnew, M.L. and R.N. Carrow. 1985. Soil compaction and moisture stress preconditioning in Kentucky bluegrass. II. Stomatal resistance, leaf water potential, and canopy temperature. Agron. J. 77:878-884.

2) Akiyama, T. and S. Kubo. 1978. Treading on the grasslands. Photosynthesis and dry matter production of native grasses. Bull. Natl. Grassl. Res. Inst. 12:23-31.

3) Alexander, C.W. and D.E. McCloud. 1962. CO_2 uptake (net photosynthesis) as influenced by light intensity of isolated bermudagrass leaves contrasted to that of swards under various clipping regimes. Crop Sci. 2:132-135.

4) Asay, K.H., C.J. Nelson, and G.L. Horst. 1974. Genetic variability for net photosynthesis in tall fescue. Crop. Sci. 14:571-574.

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

6) Brown, R.H. and W.V. Brown. 1975. Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. Crop Sci. 15:681-685.

7) --------- and V.E. Gracen. 1972. Distribution of the postillumination CO_2 burst among grasses. Crop Sci. 12:30-33.

8) --------- and R.E. Simmons. 1979. Photosynthesis of grass species differing in CO_2 fixation pathways. I.Water use efficiency. Crop Sci. 19:375-379.

9) Burian K. and C. Winter. 1976. Effect of different day-length on photosynthesis of grasses. Photosynthetica. 10:25-32.

10)Chen, T.M., R.H. Brown and C.C. Black. 1968. Photosynthetic activity of chloroplasts isolated from bermudagrass(*Cynodon dactylon*) a species with high photosynthetic capacity. Plant Physiol. 44:649-654.

11)Clark, B.J., J.L. Prioul, and H. Couderc. 1977. The physiological response to cutting in Italian ryegrass. J. British Grassl. Soc. 32:1-5.

12)Cohen, C.J., D.O. Chilcote, and R.V. Frakes. 1982. Gas exchange and leaf area characteristics of four tall fescue selections differing in forage yield. Crop Sci. 22:709-711.

13)Cooper, J.P. and D. Wilson. 1970. Variation in photosynthetic rate in *Lolium*. Proc. Int. Grassl. Congress. 11:522-527.

14)Cowling, D.W. and M.J. Koziol. 1978. Growth of ryegrass (*Lolium perenne* L.) Exposed to SO_2. I. Effects on photosynthesis and respiration. J. Exp. Bot. 29:1029-1036.

15)Davidson, I.A. and M.J. Robson. 1986. Effect of temperature and nitrogen supply on the growth of perennial ryegrass and white clover. 2. A comparison of monocultures and mixed swards. Annals of Bot. 57:709-719.

16)Deinum, B. 1976. Photosynthesis and sink size: An explanation for the low productivity of grass swards in autumn. Neth. J. Agric. Sci. 24:238-246.

17)DeMur, A.R., J.A. Swader, and V.B. Youngner. 1972. Siduron inhibition of photosystem II in isolated chloroplasts. Pest. Biochem Phys. 2:337-341.

18)Downes, R.W. and J.D. Hesketh. 1968. Enhanced photosynthesis at low oxygen concentrations: Differential response of temperate and tropical grasses. Planta (Berl.). 78:79-84

19)Downton, W.J.S. and E.B. Tregunna. 1968. Carbon dioxide compensation-its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can J. Bot. 46:207-215.

20)Duff, D.T. and J.B. Beard. 1974. Supraoptimal temperature effects upon *Agrostis palustris*. Part II. Influence on carbohydrate levels, photosynthetic rate, and respiration rate. Physiol. Plant. 32:18-22.

21)Gifford, R.M. and C. Marshall. 1973. Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. Aust. J. of Biol. Sci. 26:517-526.

22)Glacoleva, T.A. and O.V. Zalensky. 1978. Oxygen effects on photosynthesis and ^{14}C metabolism in desert plants. Plant Physiol. 62:204-209.

23)Grace, J. and J.R. Thompson. 1973. The after-effect of wind on the photosynthesis and transpiration of *Festuca arundinacea*. Physiol. Plant. 28:541-547.

24)Hart, R.H. and D.R. Lee. 1971. Age vs. net CO_2 exchange rate of leaves of Coastal bermudagrass. Crop Sci. 11:598-599.

25)Hansen, G.K. 1978. Utilization of photosynthates for growth respiration, and storage in tops and roots of *Lolium multiflorum*. Physiol. Plant. 42:5-13.

26)-----------. 1977. Adaptation to photosynthesis and diurnal oscillation of root respiration rates for *Lolium multiflorum*. Physiol. Plant. 39:275-279.

27)Hay, R.K.M. and O.M. Heide. 1983. Specific photoperiod stimulation of dry matter production in a high-latitude cultivar of *Poa pratensis*. Physiol. Plant. 57:135-142.

28)Ho, I. and J.M. Trappe. 1984. Effects of ozone exposure on mycorrhiza formation and growth of *Festuca arundinacea*. Environ. Exp. Bot. 24:71-74.

29)Hull, R.J. 1976. A carbon-14 technique for measuring photo synthate distribution in field grown turf. Agron. J. 68:99- 102.

30)---------. 1981. Diurnal variation in photosynthate partitioning in Kentucky bluegrass turf. Proc. Int. Turf. Res. Conf. 4:509-517

31)Imai, H., M. Fukuyama and T. Harada. 1973. Comparative studies on the photosynthesis of higher plants. III. Differences in response to various factors affecting the photosynthetic rate between C-4 and C-3 plants. Soil Sci. Plant Nutr. 19:61-71.

32)Jewiss, O.R. and J. Woledge. 1967. The effect of age on the rate of apparent photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Annals of Bot. 31:661-671.

33)Jones, M.B., E.L. Leafe and W. Stiles. 1980. Water stress in field-grown perennial ryegrass. I. Its effect on growth, canopy photosynthesis and transpiration. Ann. Appl. Biol. 96:87-101.

34)Joseph, M.C., D.D. Randell and C.J. Nelson. 1981. Photosynthesis in polyploid tall fescue. II. Photosynthesis and ribulose-1,5-bisphosphate carboxylase of polyploid tall fescue. Plant Physiol. 68:894-898.

35)Karnok, K.J. and J.B. Beard. 1983. Effects of gibberellic acid on the CO_2 exchange rates of bermudagrass and St. Augustinegrass when exposed to chilling temperatures. Crop Sci. 23:514-517.

36)Kaufman, J.E. and D.R. Williamson. 1981. Chemical manipulation of stomatal number and behavior in Merion Kentucky bluegrass (*Poa pratensis* L.) Proc. Int. Turf. Res. Conf. 4:501-516.

37)Krans, J.V. and J.B. Beard. 1985. Effects of clipping on growth and physiology of 'Merion' Kentucky bluegrass. Crop Sci. 25:17-20.

38)----------- and ----------. 1977. The effects of stage of developement on selected physiological and morphology parameters in Kentucky bluegrass and red fescue. Proc. Int. Turf. Res. Conf. 3:89-95.

39)Krenzer, E.G. and D.N. Moss. 1969. Carbon dioxide compensation in grasses. Crop Sci. 9:619-621.

40)Krueger, R. W. and D. Miles. 1981. Photosynthesis in fescue. III. Rates of electron transport in a polyploid series of tall fescue plants. Plant Physiol. 68:1110-1114.

41)-------------, D.D. Randall and D. Miles. 1984. Photosynthesis in tall fescue. V. Analysis of high PSI activity in a decaploid genotype. Plant Physiol. 76:903-909.

42)Labhart, C., J. Nosberger and C.J. Nelson. 1983. Photosynthesis and degree of polymerization of fructan during reproductive growth of meadow fescue at two temperatures and two photon flux densities. J. Exp. Bot. 34:1037-1046.

43)Mehall, B.J., R.J. Hull, and C.R. Skogley. 1984. Turf quality of Kentucky bluegrass cultivars and energy relations. Agron. J. 76:47-50.

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

45)Moss, D.N. 1968. Relation in grasses of high photosynthetic capacity and tolerance to atrazine. Crop Sci. 8:774.

46)Morgan, J.A. and R.H. Brown. 1983. Photosynthesis and growth of bermudagrass swards. I. Carbon dioxide exchange exchange characteristics of swards mowed at weekly and monthly intervals. Crop Sci. 23:347-352.

47)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.

48)------------and--------. 1963. Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops. Proc. Crop Sci. Soc. Japan. 31:315-321.

49)Ollerenshaw, J.H. and L.D. Incoll. 1979. Leaf photosynthesis in pure swards of two grasses (*Lolium perenne* and *Lolium multiflorum*) subjected to contrasting intensities of defoliation. Ann. Appl. Biol. 92:133-142.

50)---------------, W.S. Stewart, J. Gallimore and R.H. Baker. 1986. Low-temperature growth in grasses from northern latitudes. J. Agric. Sci. 87:237-239.

51)Ong, C.K., K.E. Colvill and C. Marshall. 1978. Assimilation of $^{14}CO_2$ by the inflorescence of *Poa annua* L. and *Lolium perenne* L. Ann. Bot. 42:855-862.

52)-------- and C. Marshall. 1975. Assimilate distribution in *Poa annua* L. Ann. Bot. 39:413-421.

53)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.

54)Peacock, C.H. and A.E. Dudeck. 1984. Physiological response of St. Augustinegrass to irrigation scheduling. Agron. J. 76:275-279.

55)Powell, A.J., R.E. Blaser and R.E. Schmidt. 1967. Physiological and color aspects of turfgrass with fall and winter nitrogen. Agron. J. 59:303-307

56)Robson, M.J. and A.J. Parsons. 1978. Nitrogen deficiency in small closed communuties of S24 ryegrass. I. Photosynthesis respiration, dry matter production and partition. Ann. Bot. 42:1185-1197.

57)Rogers, R.A., J.H. Dunn and C.J. Nelon. 1977. Photosynthesis and cold hardening in zoysia and bermudagrass. Crop Sci. 17:727-732.

58)Ruetz, W.F. 1973. The seasonal pattern of CO_2 exchange of *Festuca rubra* L. in a montane meadow community in northern Germany. Oecologia (Berl.) 13:247-269.

59)Russel, G. and J. Grace. 1978. The effect of wind on grasses. J. Exp. Bot. 29:1249-1258.

60)Sampaio, E.V.S.B., E.R. Beaty and D.A. Ashley. 1976. Bahiagrass regrowth and physiological aging. J. Rng. Manage. 29:316-319.

61)Schmidt, R.E. and R.E. Blaser. 1969. Effect of temperature, light, and nitrogen on growth and metabolism of 'Tifgreen' bermudagrass (*Cynodon* spp.) Crop Sci. 9:5-9.

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

63)----------- and V. Snyder. 1984. Effects of N, temperature, and moisture stress on the growth and physiology of creeping bentgrass and response to chelated iron. Agron. J. 76:590-594.

64)Sheehy, J.E., R.M. Green and M.J. Robson. 1975. The influence of water stress on the photosynthesis of a simulated sward of perennial ryegrass. Ann. Bot. 39:387-401.

65)Shriver, J.W. and S.W. Bingham. 1973. Selectivity of bromacil on Kentucky bluegrass and orchard grass. Crop Sci. 13:45-49.

66)------------- and ------------. 1973. Physiological effects of bromacil on Kentucky bluegrass and orchardgrass. Weed Sci. 21:212-216.

67)Silcock, R.G. and D. Wilson. 1982. The effects of leaf orientatation on photosynthesis, transpiration, and diffusive conductance of leaves of contrasting *Festuca* species. New Phytol. 90:27-36.

68)Walker, R.H. and C.Y. Ward. 1974. Influence of N and K nutrition on net photosynthesis, dark respiration, and carbohydrates in centipedegrass. Proc. Int. Turf. Res. Conf. 2:196-209.

69)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

70)--------------,-------------,------------- and ---------. 1972. Some metabolic phenomena of Kentucky bluegrass under high temperature. Crop Sci. 12:87-90.

71)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.

72)Wilson, D. 1975. Leaf growth, stomatal diffusion resistances and photosynthesis during droughting of *Lolium perenne* populations selected for contrasting stomatal length and frequency. Ann. Appl. Biol. 79:67-82.

73)---------- and J.P. Cooper. 1969. Apparent photosynthesis and leaf characters in relation to leaf position and age, among contrasting *Lolium* genotypes. New Phytol. 68:645-655.

74)Winstead, C.W. and C.Y. Ward. 1974. Persistence of southern turfgrasses in a shade environment. Proc. Int. Turf. Res. Conf. 2:221-230.

75)Woledge, J. 1979. Effect of flowering on the photosynthetic capacity of ryegrass leaves grown with or without natural shading. Ann. Bot. 44:197-207.

76)----------. 1978. The effect of shading during vegetative and reproductive growth on the photosynthetic capacity of leaves in a grass swards. Ann. Bot. 42:1085-1089.

77)----------. 1977. The effects os shading and cutting treatments on the photosynthetic rate of ryegrass leaves. Ann. Bot. 41:1279-1286.

78)---------- and W.D. Dennis. 1982. The effect of temperature on photosynthesis of ryegrass on white clover leaves. Ann. Bot. 50:25-35.

79)---------- and O.R. Jewiss. 1969. The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann. Bot. 33:897-913.

80)---------- and E.L. Leafe. 1976. Single leaf and canopy photosynthesis in a ryegrass swards. Ann. Bot. 40:773-783.

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

82)Yang, Y. and S.W. Bingham. 1984. Effects of metribuzin on net photosynthesis of goosegrass (*Eleusine indica*) and bermudagrass (*Cynodon* spp.). Weed Sci. 32:247-250.

83)Youngner, V.B., F. Nudge and R. Ackerson. 1976. Growth of Kentucky bluegrass leaves and tillers with and without defoliation. Crop Sci. 16:110-113.

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 $\mu L\ L^{-1}$, 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 $\mu mol\ m^{-2}\ s^{-1}$. 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

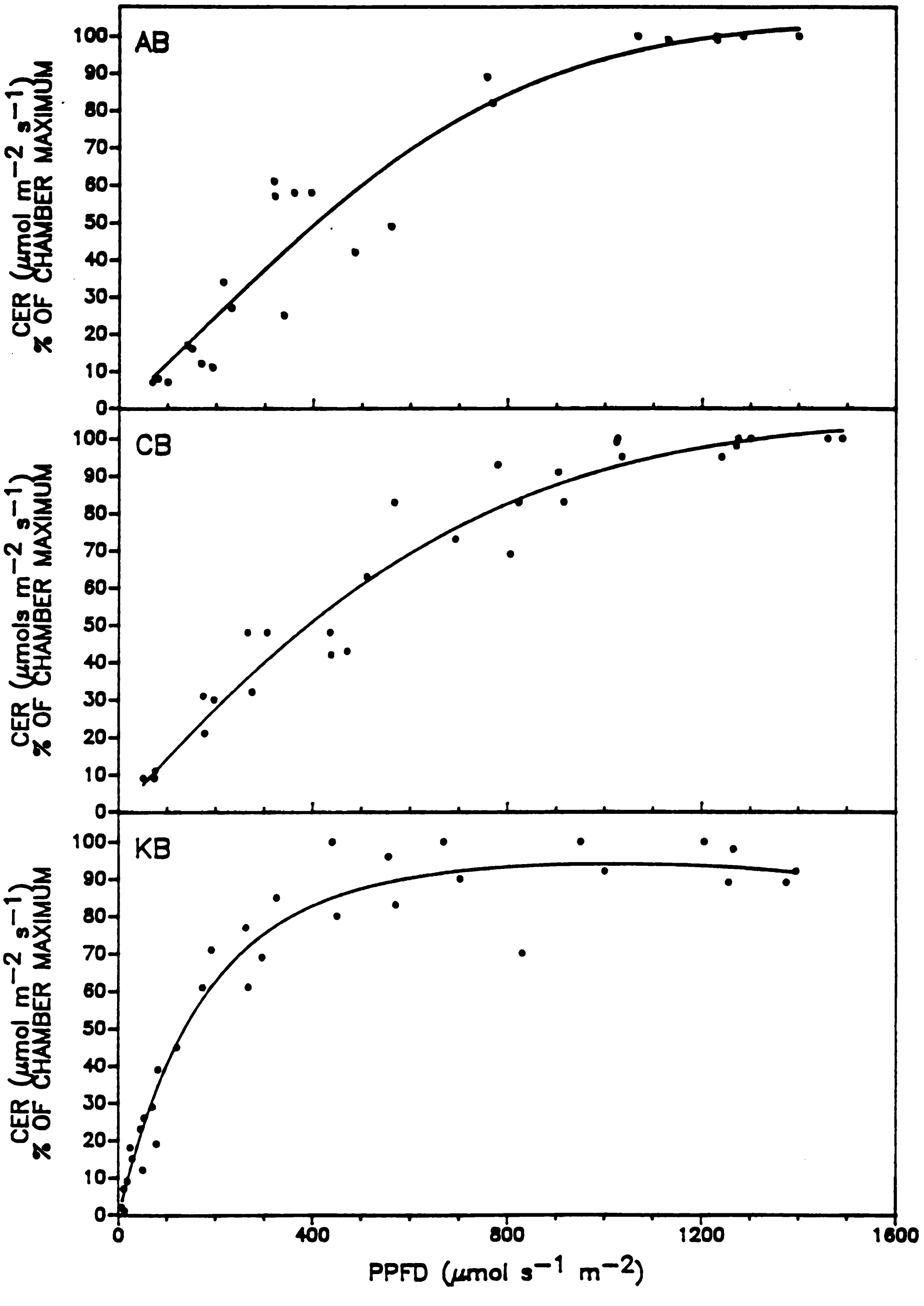

Figure 1. Effect of photosynthetic photon flux (PPF) on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB, R^2=0.95), creeping bentgrass (CB, R^2=0.95)and annual bluegrass (AB, R^2=0.92). Measurements were made at chamber temperature of 21°C and atmospheric CO_2 concentrations.

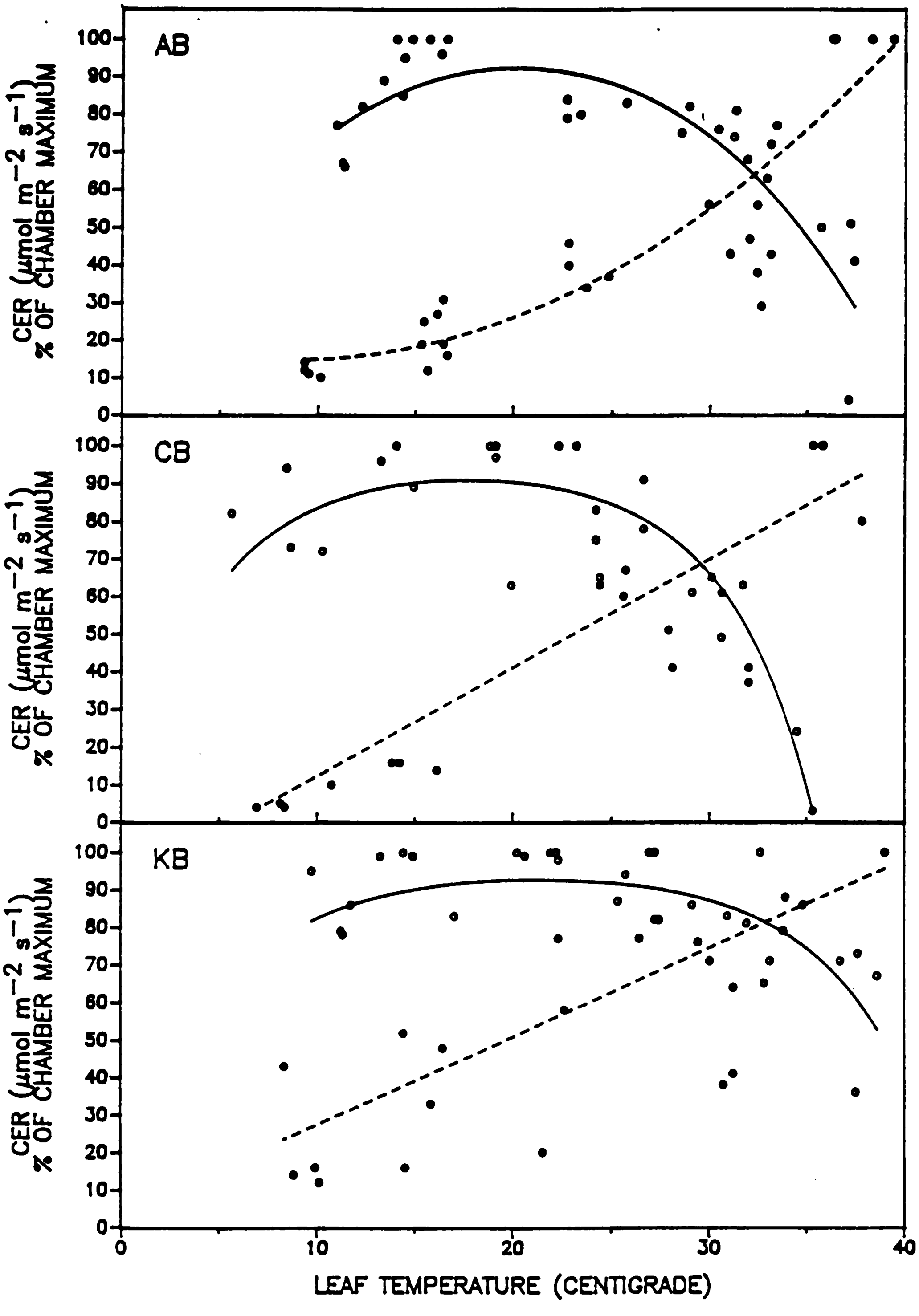

Figure 2. Effect of leaf temperature on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB), creeping bentgrass (CB) and annual bluegrass (AB). Net photosynthesis (solid line, open circle) measured at >1000 umol m^{-2} s^{-1} light intensity. CER and dark respiration (dashed line, closed circle) measured 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.

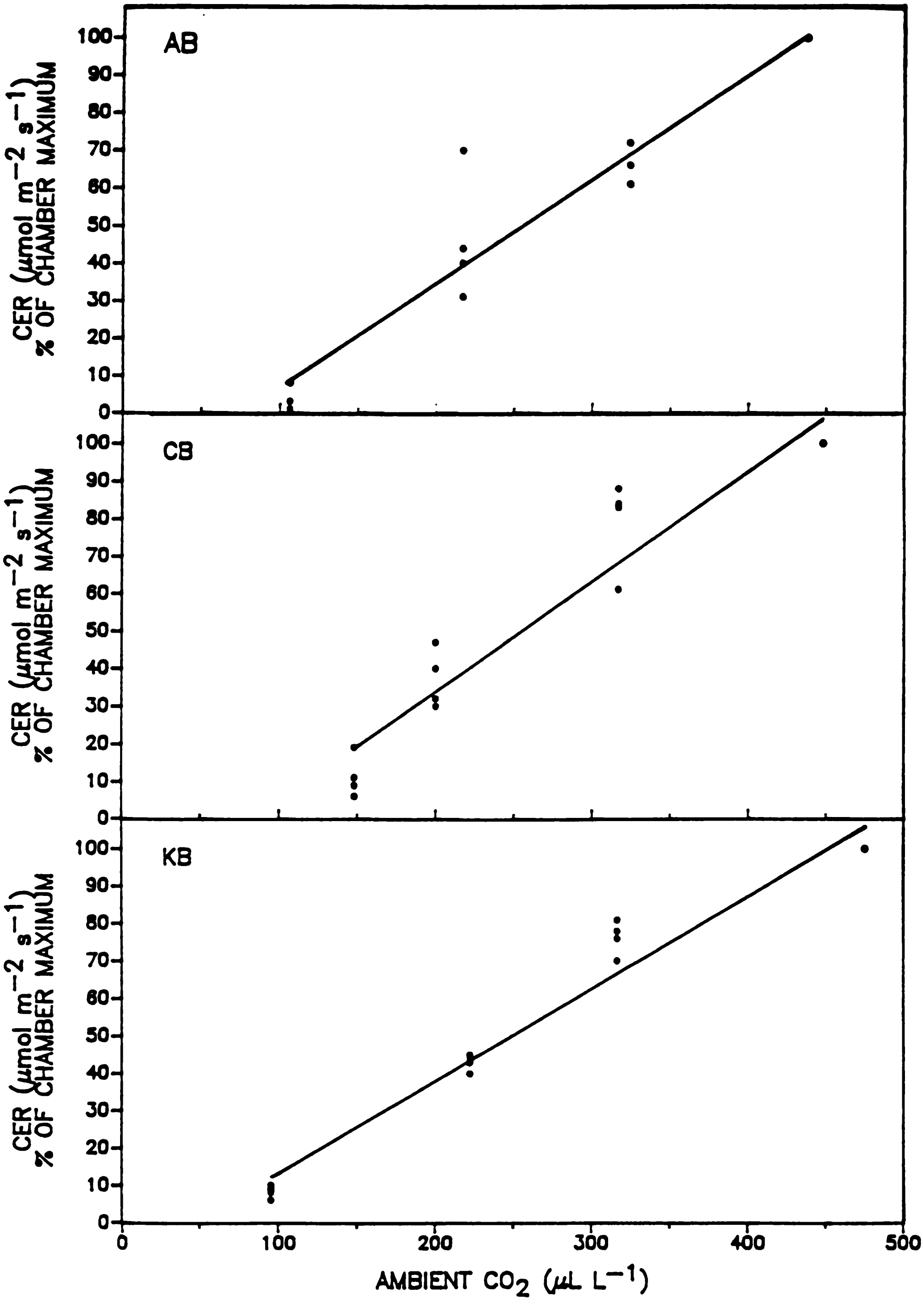

Figure 3. Effect of ambient CO_2 concentration on CO_2 Exchange Rate (CER) of Kentucky Bluegrass (KB), creeping bentgrass (CB) and annual bluegrass (AB). All measurements obtained at >1000 umol m^{-2} s^{-1} light intensity and chamber temperature of 21°C. R^2 = 0.97, 0.92, and 0.93 for KB, CB, and AB,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

<u>Species Comparison.</u> 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.

NET PHOTOSYNTHESIS AND CHLOROPHYLL CONTENT AS AFFECTED BY SYNTHETIC PLANT GROWTH REGULATORS

ABSTRACT

Research was conducted to determine the effects of the synthetic plant growth regulators mefluidide and EL-500 on net photosynthesis, total chlorophyll, and dry weight/unit leaf area of annual bluegrass (*Poa annua* var. *reptans* (Hausskn.) Timm.) and creeping bentgrass (*Agrostis palustris* Huds cv. 'Penncross'). Plants were treated with mefluidide at 0.00, 0.14, 0.28, and 0.56 kg ha^{-1} or EL-500 at 0.00, 1.12, 2.24, and 4.48 kg ha^{-1} and data was collected 9 days after treatment (DAT) for mefluidide treatments and 10 DAT for EL-500 treatments. EL-500 rates decreased carbon dioxide exchange rate (CER) of annual bluegrass 38% compared to untreated plants, while creeping bentgrass CER was unaffected by EL-500 rates. EL-500 increased the total chlorophyll of creeping bentgrass 20% over untreated plants. Increasing rates of mefluidide had no effect on photosynthesis of either species but did increase total chlorophyll 83% and dry weight/unit area 37% over untreated plants. In a separate study, both species were treated with

mefluidide at 0.00 and 0.28 kg ha^{-1} or EL-500 at 0.00 and 2.24 kg ha^{-1} and data were collected 4, 8, 16, 32, and 64 days after treatment (DAT). Mefluidide inhibited CER of both species 4 and 8 DAT after treatment. Inhibition 4 DAT, averaged across species, was 44% and at 8 DAT, 55% compared to untreated plants. El-500 inhibited both species 58% 16 DAT. Both compounds increased total chlorophyll 16 DAT. Mefluidide increased chlorophyll 80%, while the EL-500 increase was 51%. Both compounds inhibit photosynthesis and increase total chlorophyll under qualifying conditions. Further research into specifics of these alterations and possible reversal of treatment effects with exogenous gibberellic acid applications warrants attention.

INTRODUCTION

Plant growth regulators (PGR's) are currently receiving a great deal of attention in turfgrass industry and research. The uses for PGR's in turf range from vegetative control of highway roadside grasses to seedhead suppression and species conversion on intensively managed golf course turf. However, inconsistencies in efficacy and lack of information on physiological effects imposed by PGR application has prompted research interest on PGR effects on turfgrass physiological properties.

Mefluidide (N-[2,4-dimethyl-5 [[(trifluoromethyl) sulfonyl] amino] phenyl] acetamide) and EL-500 (α-(1-methylethyl)- α-[4-trifluoro methoxy)phenyl] 5-pyrimidine methanol) are synthetic PGR's currently utilized in turfgrass management. Physiologically, mefluidide and EL-500 are known to inhibit gibberellin biosynthesis by blocking ent-kaurene oxidation (34) which ultimately inhibits cell elongation. Further, mefluidide has been shown to influence the polar transport of IAA (16). Specifically on turfgrass species mefluidide is known to inhibit seedhead production of annual bluegrass (*Poa annua* L.) (7,28) and increase root elongation and depth of rooting of annual bluegrass (7). In Kentucky bluegrass (*Poa pratensis* L.) mefluidide has been found to reduce root and tiller production but increase rhizome length (5,12,14,31), while EL-500 increases tiller production (10). EL-500 is reported to exhibit selective growth suppression of annual bluegrass in mixed stands with perennial ryegrass (*Lolium perenne* L.) (3) or creeping bentgrass (*Agrostis palustris* Huds.) (32). Additionally, both PGR's have been shown to alter photosynthate partitioning in Kentucky bluegrass (18). Visual effects of turfgrasses treated with mefluidide or EL-500 range from an initial loss in quality due partially to phytotoxicity to an eventual increase in quality due in part to enhancement of green color (4,7,15,22,28). The reported turf quality and morphological effects and differences in photosynthate partitioning indicates the possibility of an alteration in a physiological process such as carbon dioxide assimilation and/or chlorophyll synthesis. The objectives of this research were to evaluate the effect of mefluidide and EL-500 applications on the net photosynthesis, total chlorophyll and leaf dry weight/unit area of annual bluegrass and creeping bentgrass.

MATERIALS AND METHODS

Plant Material. Tillers were obtained from mature stands of annual bluegrass and creeping bentgrass located at the Hancock Turfgrass Research Center, East Lansing, MI and transplanted into styrofoam cups. The growth medium was 5 sandy loam : 3 sand : 1 peat moss (by volume). Plants were grown in the greenhouse where temperatures fluctuated between 16 and 24 °C. Plants were watered twice daily with an automatic misting system and fertilized weekly with 55 mg urea in 50 ml tap water (0.28 kg ha^{-1}).

Net Photosynthesis Determination. Net photosynthesis was measured using a open gas analysis system previously described by Augustine et al. (2) as modified by Sams and Flore (30). Measurements were made on 5 to 15 leaves placed into the assimilation chamber such that leaf to leaf shading was minimal. Immature and senescing leaves were excluded from the chamber to ensure maximum gas exchange. Assimilation chamber conditions were; ambient temperature of 21 °C, ambient CO_2 between 320 and 345 $\mu L\ L^{-1}$, light intensity of > 1000 $\mu mol\ m^{-2}\ s^{-1}$ and leaf to air vapor pressure deficits < 1.5 KPa. Net photosynthesis was calculated as a molar flux, using the mole fraction of CO_2 as suggested by Cowen (8). Net photosynthesis was calculated on a leaf area basis using basic computer programs designed by Moon and Flore (23).

Chlorophyll Determination. Chlorophyll was extracted from fresh leaf material using *N*,*N*-dimethylformamide as described by Moran and Porath (24). Samples were maintained in the dark at 4-5 °C for 48 hrs prior to analysis on a Beckman spectrophotometer. Total chlorophyll was calculated based on extinction coefficients determined by Inskeep and Bloom (19). Chlorophyll was expressed on a leaf area basis.

Leaf Dry Weight/Unit Area. One day prior to determination of net photosynthesis 5 to 10 leaves were clipped from each plant sample and the leaf area determined on a Li-Cor leaf area meter. Leaves were then dried in a forced air dryer at 65 °C for 48 hrs and dry weight recorded. The leaf area and dry weight data were used to determine mg dry weight per cm^2 leaf area. Additionally this data was used to calculate total chlorophyll on a dry weight basis.

Rate Study

Plants were treated with mefluidide at 0.00, 0.14, 0.28, and 0.56 kg ha^{-1} or EL-500 at 0.00, 1.12, 2.24, and 4.48 kg ha^{-1} . Treatments were applied via a conveyor belt sprayer equipped with an 8002E nozzle calibrated to deliver 770 L ha^{-1} at 0.21 MPa. Net photosynthesis, total chlorophyll and dry weight/unit area were determined as previously described. Data were collected for mefluidide treatments 10 days after treatment (DAT) and EL-500 treatments nine DAT. Data collected were expressed as a percent of the control rate and the two compounds were analyzed separately. Treatment design was a 2 (species) X 4 (rate) factorial. The mefluidide rate study utilized four replications and the EL-500 rate study, five replications. An analysis of variance (AOV) was calculated for each variable and means separated with the least significant difference (LSD) multiple comparison technique.

Time Course Study

Plants were treated with mefluidide at 0.00 and 0.28 kg ha^{-1} or EL-500 at 0.00 and 2.24 kg ha^{-1} . Treatments were applied as described in the rate study. Data were collected on net photosynthesis and total chlorophyll 4, 8, 16, 32 and 64 DAT. Data collected were expressed as a percent of the control rate and the two compounds were analyzed separately. Treatment design was a 2 (species) X 2 (rate) factorial with 4 replications. An AOV was calculated for each evaluation date and means separated by the LSD multiple comparison technique.

RESULTS

Rate Study

EL-500. Results of the AOV found species and EL-500 rates to be significant sources of variability. As rate increased net photosynthesis of both species declined (Figure 4). However, the net photosynthesis of creeping bentgrass was never significantly affected by EL-500 rates when compared to the control while rates of 2.24 and 4.56 kg ha^{-1} significantly inhibited photosynthesis of annual bluegrass.

When expressed on a dry rate basis EL-500 rates significantly affected total chlorophyll, but when expressed on a leaf area basis total chlorophyll was not affected. Species did not differ in their response to rates of EL-500, when chlorophyll was expressed on a dry weight basis (Figure 4). However, species were significantly different when chlorophyll was expressed on a leaf area basis. When the data for net photosynthesis and total chlorophyll (leaf area) are averaged across EL-500 rates photosynthesis of annual bluegrass was significantly reduced and total chlorophyll of creeping bentgrass increased when compared to the control (Figure 5).

Mefluidide. Total chlorophyll was significantly affected by mefluidide rate but not by species when expressed on a leaf area or dry weight basis. The trend was for increased total chlorophyll from 0.00 to 0.28 kg ha^{-1} with significant differences for both parameters at 0.28 kg ha^{-1}. Total chlorophyll appeared to decline at 0.56 kg ha^{-1} but did not differ from the control (Figure 6). Mefluidide rates significantly affected dry weight/unit area equally for both species with an increase in dry weight/unit area as rate increased (Figure 6).

Time Course Study

EL-500. Results of the AOV found no significant differences between species for net photosynthesis on any of the measurement dates. Photosynthesis, averaged across species, gradually declined from 4 to 16 DAT with a significant

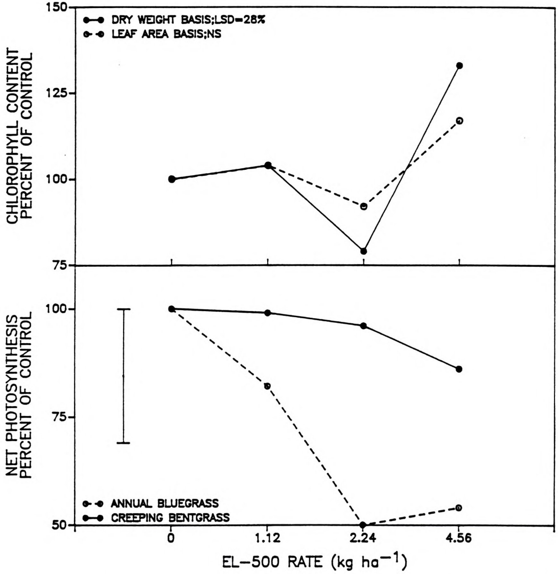

Figure 4. Effect of EL-500 rates on net photosynthesis of annual bluegrass and creeping bentgrass (vertical bar represents LSD at P=0.05) and chlorophyll content (mean of both species). Rate effect on chlorophyll content was non-significant (NS) on a leaf area basis and significant (P=0.05) on a dry weight basis.

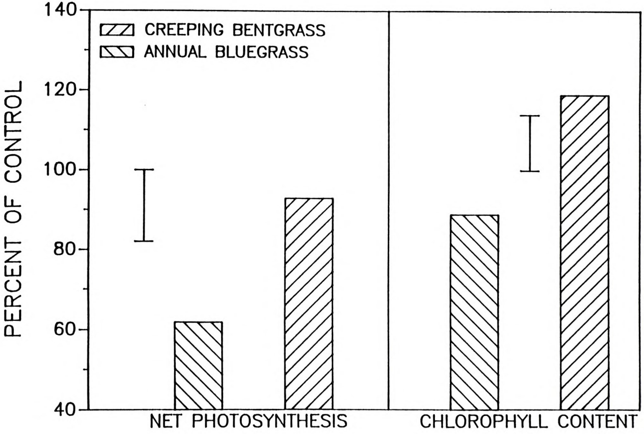

Figure 5. Effect of EL-500 on net photosynthesis and chlorophyll content (leaf area basis). Vertical bars represents LSD (P=0.05). Data for each species averaged across 3 rates of EL-500.

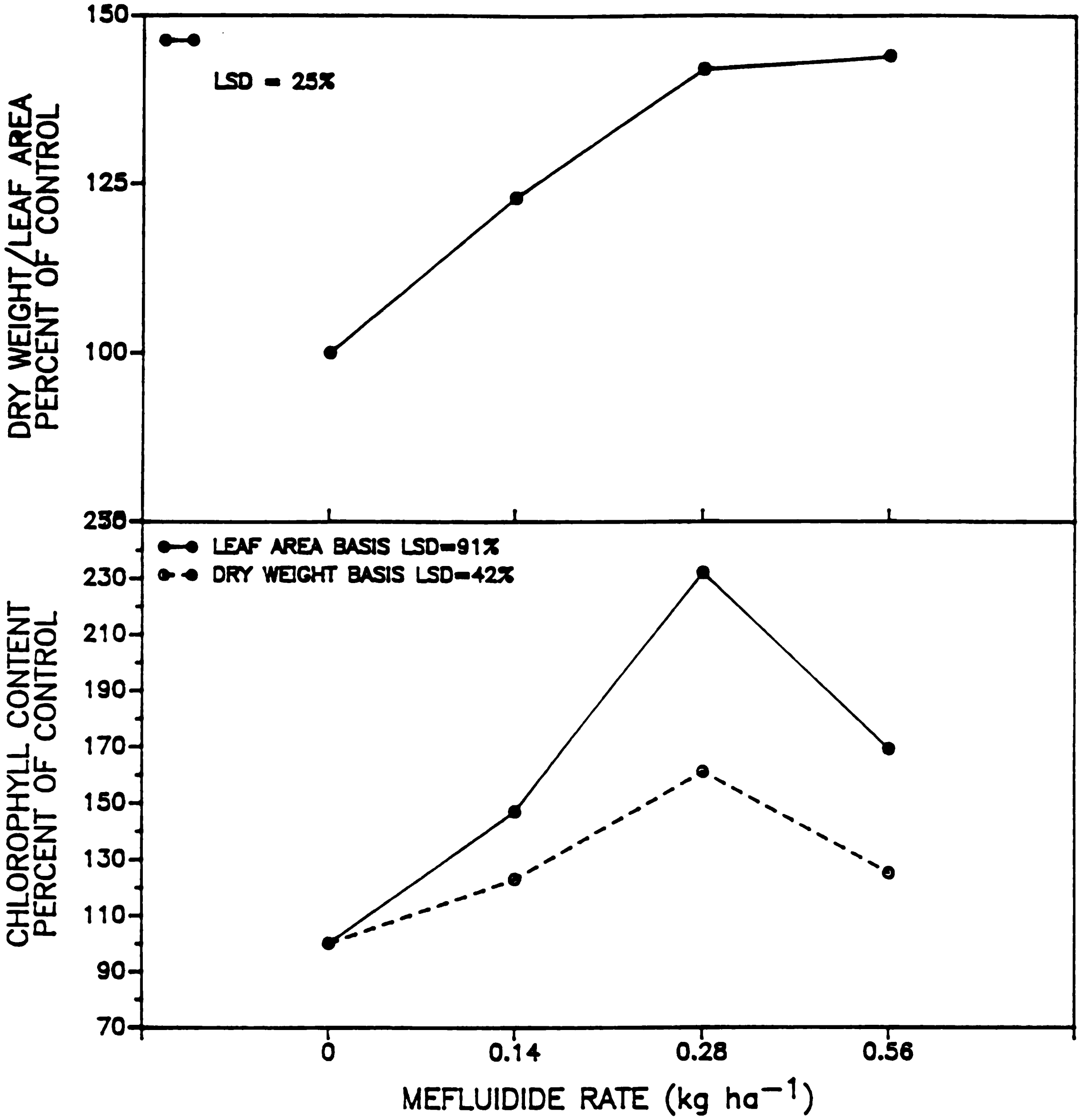

Figure 6. Effect of mefluidide rates on chlorophyll content and dry weight/unit leaf area of annual bluegrass and creeping bentgrass. Data points represent mean of both species.

difference between the EL-500 treated plants and the control on the 16 DAT measurement date. On the 32 and 64 DAT measurement photosynthesis was higher in the treated plants but not significantly different from the control (Figure 7). The total chlorophyll of treated plants was significantly affected at 16 DAT (Figure 7). A difference between species was also noted on this date with with annual bluegrass having a total chlorophyll 133% and creeping bentgrass 167% of their respective control plants.

Mefluidide. Results of the AOV found no significant differences between species for net photosynthesis on any of the measurement dates. On the 4 and 8 DAT measurement dates photosynthesis, when averaged across species, was significantly reduced by mefluidide treatment (Figure 7). As was seen with EL-500 treated plants at 16 DAT mefluidide treated plants had a significantly higher total chlorophyll than control plants (Figure 7).

DISCUSSION

Both El-500 and mefluidide were found to inhibit photosynthesis. As EL-500 rate increased net photosynthesis decreased. No rate effect was shown for mefluidide when measured at 9 DAT. However in the time course study, mefluidide at 0.28 kg ha^{-1} significantly inhibited photosynthesis 4 and 8 DAT, while EL-500 treated plants were significantly inhibited 16 DAT. It appears that the window of inhibition is extremely narrow for both compounds and the lack of a significant rate effect for mefluidide might be

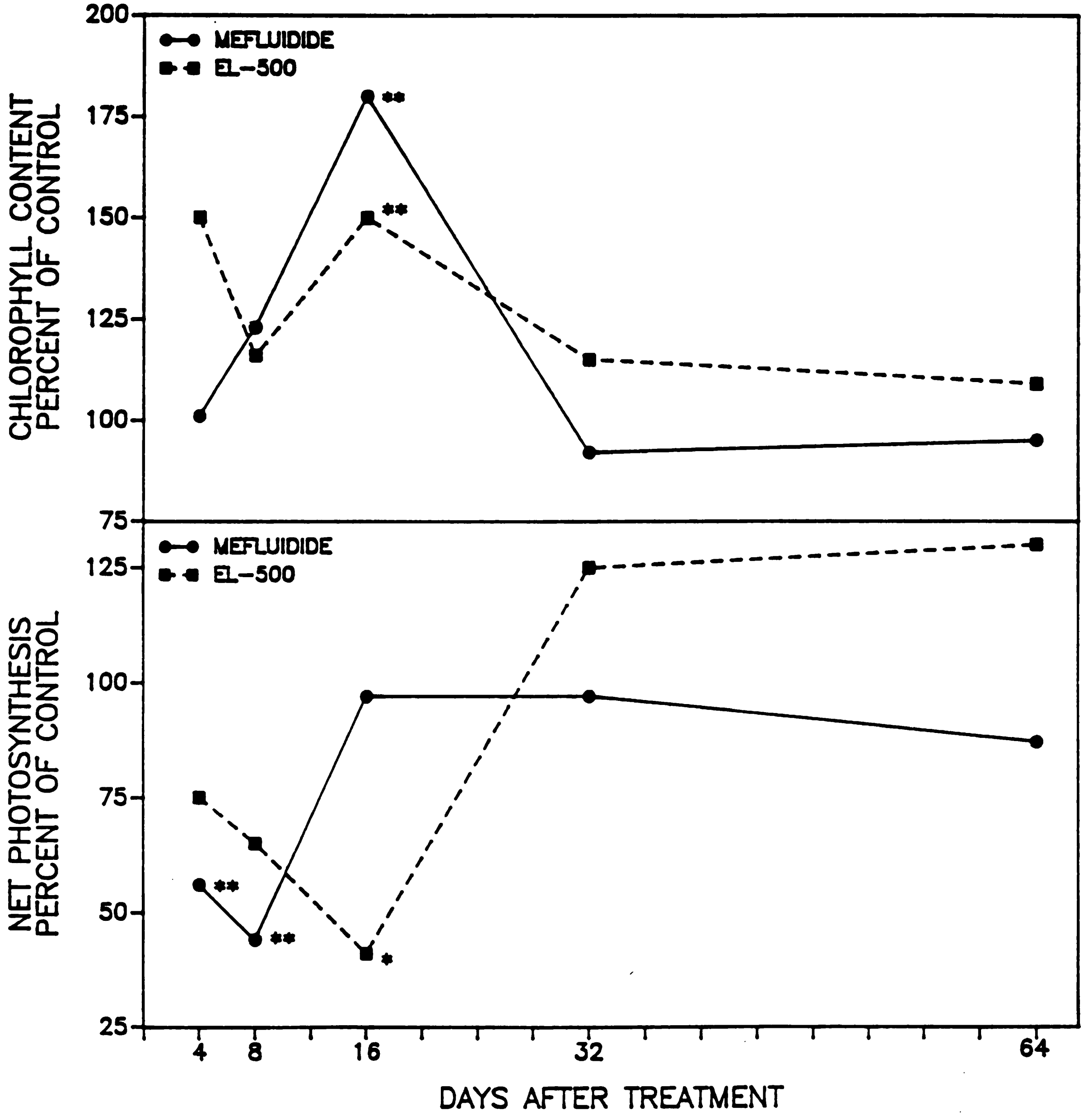

Figure 7. Effect of EL-500 and mefluidide on net photosynthesis and chlorophyll content (leaf area basis) of annual bluegrass and creeping bentgrass. Data points represent mean of both species. Asterisks adjacent to data point indicate significant difference between control and PGR treatment on respective evaluation date. * and ** indicate significance at P=0.05 or P=0.01 respectively.

explained by data being collected after the inhibition window. The early inhibition of photosynthesis by mefluidide versus the relatively late inhibition by EL-500 is probably due to contrasting modes of uptake for these two compounds. Mefluidide is primarily foliar absorbed (13) whereas EL-500 is primarily root absorbed (ELANCO Products Co., 1983,personal communication). The foliar absorbed mefluidide would be absorbed faster than the EL-500 hence the inhibition is exhibited earlier.

Mefluidide and EL-500 are known to inhibit gibberellic acid (GA) biosynthesis (6,16). Studies have indicated that GA's might be considered photosynthesis promoters (9). Exogenous applications of GA_3 to the roots of tomato (*Lycopersicon* spp.) plants has been shown to increase leaf photosynthesis (1). Application of GA_3 to foliage of 'Ormond' and 'Pee Dee' bermudagrass (*Cynodon dactylon* [L.] Pers.) (21) has been shown to increase net photosynthesis, after these two cultivars were grown at chilling temperatures. However, it does not appear that GA directly affects electron transport because studies have shown no increase in photosynthetic activity of isolated chloroplasts treated with GA (29). Additionally GA's have been shown to alter sink strength in sunflower (*Helianthus annuus* L.) (33) and alter sink strength and increase acid invertase activity in bean (*Phaseolus vulgaris* L.) (25). Altered sink strength or assimilate accumulation has been shown to affect photosynthesis in plants (27) and specifically in grasses (17,26). Although studies are limited it does appear that GA's act as photosynthesis promoters. Conversely a compound which inhibits GA biosynthesis, such as mefluidide or EL-500, may inhibit photosynthesis by reducing endogenous levels of GA.

El-500 exhibited selectivity in inhibition of photosynthesis and effect on chlorophyll concentration in annual bluegrass and creeping bentgrass. Net photosynthesis and total chlorophyll of annual bluegrass were decreased by EL-500 treatment while creeping bentgrass was unaffected. Field applications of EL-500 have been reported to selectively suppress growth of annual bluegrass in mixed stands with perennial ryegrass (3) or creeping bentgrass (32).

Based on results of dry weight/unit area data increasing rates of mefluidide increased leaf thickness of both species. This increase in leaf thickness was reflected in the chlorophyll data. Whether expressed on a leaf area or dry weight basis mefluidide increased total chlorophyll, however the response was more pronounced on a leaf area basis. In mefluidide treated plants it appears that the increase in total chlorophyll is primarily an increase reflected in an increased leaf width. The same response was not shown for EL-500. However, Devlin and Kosanski (11) reported a increase in leaf thickness in corn leaves following EL-500 treatment. Examination of the AOV finds the level of significance for this attribute to be P = 0.09. If the arbitrary level for significance is increased to 0.1 then the increase in total chlorophyll in EL-500 treated plants is not a reflection of the increase in leaf width.

Both compounds investigated altered the physiological and morphological attributes evaluated. Further research is necessary to investigate the extent of these alterations. Possible avenues of investigation might include direct effects of PGR's on O_2 evolution in isolated chloroplasts and reversal of treatment effects by exogenous application of GA.

REFERENCES

1) Arteca, R. N. and C.N. Dong. 1981. Increased photosynthetic rate following gibberellic acid treatments of tomato plants. Photosynthesis Res. 2:243-249.

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

3) Breuninger, J.M., T.L. Watschke. 1982. Post emergent *Poa annua* control with growth retardents. p.314. *In* Proc. 36th Meeting Northeastern Weed Sci. Soc. New York, NY. 5-7, Jan. 1982. Evans Printing, Inc. Salisbury, MD.

4) Breuninger, J.M., T.L. Watschke, and L.D. Tukey. 1983. Effect of PP-333 and flurprimidol (EL-500) on tall fescue in an apple orchard. p. 370. *In* Proc. 37th Meeting Northeastern Weed Sci. Soc. Grossinger, NY. 4-6, Jan. 1983. Evans-Coates Printing, Inc. Salisbury, MD.

5) Christians, N.E. and J. Nau. 1984. Growth retardent effects on three turfgrass species. J. Am. Soc. Hort. Sci. 109:45-47.

6) Coolbaugh, R.C., D.I. Swanson and C.A. West. 1982. Comparative effects of ancymidol and its analogs on growth of peas and *Ent*-kaurene oxidation in cell free extracts of immature *Marah macrocarpus* endosperm. Plant Physiol. 69:707-711.

7) Cooper, R.J., P.R. Henderlong, J.R. Street and K.J. Karnok. 1987. Root growth, seedhead production, and quality of annual bluegrass as affected by mefluidide and a wetting agent. Agron. J. 79:929-934.

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

9) Davies, P.J. 1987. Plant hormones and their role in plant growth and developement. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.

10)Dernoeden, P.H. 1984. Four-year response of Kentucky bluegrass-red fescue turf to plant growth retardents. Agron. J. 76:807-813.

11)Devlin, R.M. and Z.K. Koszanski. 1985. The effect of paclobutrazol and flurprimidol on pigment and biomass synthesis. Proc. Plant Growth Reg. Soc. Amer. 12:243-247.

12)Elkins, D.M., J.W. Vandeventer, and M.A. Briskovich. 1977. Effect of chemical growth retardents on turfgrass morphology. Agron. J. 69:458-461.

13)Field, R.J. and A.R. Whitford. 1982. Effect of simulated mowing on the translocation of mefluidide in perennial ryegrass (*Lolium perenne* L.). Weed Research. 22:177-181

14)Freeborg, R.P., and W.H. Daniel. 1981. Growth regulation of *Poa pratensis* L. p. 477-486. *In* Fourth Int. Turgrass Res. Conf. Proc. Guelph, Ontario. Univ. of Guelph, Guelph Ontario.

15)Gaussoin, R.E., B.E. Branham, and P.E. Rieke. 1985. Cultural factors in annual bluegrass and creeping bentgrass competition. p. 35-37. *In* Proc. 55th Annual Mich. Turfgrass Conf. Lansing, MI 21-23, Jan. 1985. Mich. Turf Found., Mich Ag. Expt. Sta. and Coop. Ext. Service, Michigan State Univ. East Lansing, MI.

16)Glenn,S. and C.E. Rieck. 1985. Auxinlike activity and metabolism of mefluidide in corn (*Zea mays*) and soybean (*Glycine max*) tissue. Weed Sci. 33:452-456.

17)Hansen, G.K. 1978. Utilization of photosynthates for growth, respiration, and storage in tops and roots of *Lolium multiflorum*. Physiol. Plant. 42:5-13.

18)Hanson, K.V. and B.E. Branham. 1987. Effects of four growth regulators in photosynthate partitioning in 'Majestic' Kentucky bluegrass. Crop Sci. 27:1257-1260.

19)Inskeep, W.P. and P.R. Bloom. 1985. Extinction coefficients of chlorophyll *a* and *b* in *N,N*-dimethylformamide and 80% acetone. Plant Physiol. 77:483-485.

20)Jones, R. L. and J. MacMillan. 1984. Gibberellins. p.21-52. *In* M.B. Wilkins (ed.) Advanced Plant Physiology. Pitman Publishing Inc., Marshfield, MA.

21)Karnok, K.J. and J.B. Beard. 1983. Effects of gibberellic acid on the CO_2 exchange rates of bermudagrass and St. Augustinegrass when exposed to chilling temperatures. Crop Sci. 23:514-517

22)McCarty, L.B., J.M. DiPaola, W.M. Lewis and W.B. Gilbert. 1985. Tall fescue response to plant growth retardents and fertilizer sources. Agron. J. 77:476-480.

23)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.

24)Moran, R. and D. Porath. 1980. Chlorophyll determination in intact tissue using *N,N*-dimethylformamide. Plant Physiol. 65:478-479.

25)Morris, D.A. and E.D. Arthur. 1985. Effects of gibberellic acid on patterns of carbohydrate distribution and acid invertase activity in *Phaseolus vulgaris*. Physiol. Plant. 65:257-262.

26)Moss, D.N. 1962. Photosynthesis and barrenness. Crop Sci. 2:366-367.

27)Neales, T.F. and L.D. Incoll. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. Bot. Rev. 34:107-125.

28)Petrovic, A.M., R.A. White and M. Kligerman. 1985. Annual bluegrass growth and quality as influenced by treatments of growth retardents and wetting agents. Agron. J. 77:670-674.

29)Robinson, S.P., J.T. Wiskich and L.G. Paleg. 1978. Effects of indoleacetic acid on carbon dioxide fixation, electron transport and phosphorylation in isolated chloroplasts. Aust. J. Plant Phys. 5:425-431.

30)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.

31)Schmidt, R.E. and S.W. Bingham. 1977. Chemical growth regulation of 'Baron' Kentucky bluegrass. Agron. J. 69:995-1000.

32)Shoop, G.L., R.H. Hoefer and D.G. Ortega. 1986. Flurprimidol (EL-500) growth regulator effect on bentgrass fairways in the northeast. p. 131. *In* Proc. 40th Annual Meeting Northeastern Weed Sci. Soc. Boston, MA. 7-9, Jan. 1986. Evans-Coates Printing, Inc. Salisbury, MD.

33)Umossien, S.N. and D.F. Forward. 1982. Effects of gibberellic acid on the distribution of products of photosynthesis in sunflower. Ann. Bot. 50:465-472.

34)Wilkinson, R.E. 1982. Mefluidide inhibition of sorghum growth and gibberellin precursor biosynthesis. J. Plant Growth Regul. 1:85-94.

APPENDIX

Table A1. Clipping removal effects on tissue mineral concentrations of an annual bluegrass/creeping bentgrass mixture.

Clipping Treatment	Element											
	N	P	K	Ca	Mg	Mn	Fe	B	Cu	Zn	Al	
	%	mg kg^{-1} (x10)										
	sampled 6 June,1986											
Removed	4.0	488	2451	517	270	7.8	10.4	0.8	0.8	5.2	3.9	
Returned	4.3	509	2751	493	287	8.3	10.5	0.9	1.1	6.3	3.6	
	sampled 25 Oct,1986											
Removed	4.1	477	1063	---	447	14	20.3	0.4	0.9	5.8	30	
Returned	4.2	493	1100	---	460	15	21.3	0.4	0.9	4.5	33	

Table A2. Clipping removal and N-Fertility effects on soil mineral concentrations.

Clipping Treatment	Element							
	NO_3-N	P	K	Ca	Mg	Zn	Cu	Mn
	mg kg^{-1}	kg ha^{-1}				mg kg^{-1}		
	sampled 21 June,1985							
Removed	---	133	96	2346	347	5	4	36
Returned	---	129	145	2522	343	7	4	40
	sampled 27 Oct, 1986							
Removed	2.8	74	87	1854	379	-	-	-
Returned	3.7	75	113	2008	377	-	-	-
N-Fertility kg ha^{-1} yr^{-1}								
98	2.8	81	120	1854	362	-	-	-
293	3.6	68	79	2008	394	-	-	-

Table A3. Raw data for regression analysis of diurnal effects on CER of Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
Time+	CER++	Time	CER	Time	CER
7.62	13.97	7.72	3.73	8.00	9.42
7.70	14.55	7.80	5.54	8.13	13.03
7.80	7.20	7.92	8.23	8.22	13.77
7.90	12.26	8.07	5.71	8.25	9.78
8.52	14.33	8.47	3.97	8.78	9.94
8.60	15.00	8.55	5.63	8.95	13.14
8.67	7.73	8.65	8.08	9.07	13.74
8.75	13.08	8.77	6.28	9.20	10.59
9.73	16.83	9.58	5.62	9.47	12.11
9.83	16.11	9.68	8.22	9.88	14.83
9.95	8.98	9.78	6.41	10.00	14.79
10.05	15.34	9.83	3.57	10.20	11.77
10.77	17.68	10.72	5.02	10.75	11.86
10.88	17.25	10.82	6.21	10.83	15.00
11.00	10.84	10.95	9.08	10.98	14.85
11.13	13.49	11.02	6.30	11.08	11.94
11.85	19.07	11.95	4.58	11.96	12.25
11.97	16.02	12.17	6.12	12.20	15.31
12.05	9.72	12.32	8.92	12.33	14.81
12.12	15.39	12.45	6.65	12.50	12.36
12.95	18.24	13.85	6.03	13.32	14.75
12.85	17.38	13.80	4.54	13.38	12.36
13.02	10.08	14.02	6.51	13.32	14.75
13.12	13.33	14.18	6.88	13.67	14.58
14.42	16.96	14.77	5.25	13.78	11.15
14.50	16.51	14.88	6.29	14.65	12.22
14.57	9.31	15.00	9.00	14.70	15.67
14.67	14.69	15.06	6.90	14.92	14.73
15.55	16.64	15.92	5.13	15.08	11.72
15.65	16.29	16.12	6.12	15.60	12.26
15.78	9.38	16.32	9.37	15.70	14.97
15.88	15.23	16.37	6.83	15.88	14.23
16.45	17.14	16.92	5.12	16.02	12.15
16.57	15.17	17.00	6.12	16.58	11.83
16.70	10.33	17.08	9.05	16.67	14.59
16.76	14.86	17.15	6.75	16.80	14.08
17.23	16.46	17.38	5.25	16.88	11.35
17.38	16.06	17.47	6.00	17.30	12.17
17.55	10.32	17.58	8.90	17.37	14.62
17.72	16.20	17.77	6.31	17.47	13.83
				17.53	11.40
				17.63	12.13
				17.75	14.99
				17.83	13.96
				18.00	11.48

\+ Decimal time of day

++ Carbon Dioxide Exchange Rate (μmol m^{-2} s^{-1})

Table A4. Raw data for regression analysis of PPF (mol m^{-2} $^{s-}$1) effects on CER of Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
PPF	CER+	PPF	CER	PPF	CER
7	0.52	50	1.22	68	0.88
11	1.58	74	1.11	80	1.02
13	0.02	75	1.38	100	0.96
18	1.15	174	4.04	140	2.23
24	3.87	177	2.71	150	2.03
28	1.36	196	3.88	169	1.61
45	2.14	265	6.24	192	1.31
50	1.37	274	4.18	214	4.42
52	5.72	305	6.22	231	3.22
70	3.78	435	8.85	318	7.98
78	2.17	437	5.41	320	6.91
81	8.54	470	5.64	339	3.30
120	5.10	510	7.79	360	7.42
173	13.33	567	10.76	395	7.47
191	9.17	692	8.96	485	5.12
262	16.80	780	11.44	560	6.40
267	7.01	805	8.90	757	10.80
295	8.93	823	10.78	769	10.65
325	18.50	915	10.84	1067	12.13
440	9.30	1024	12.18	1130	12.80
450	9.11	1026	12.93	1230	13.01
555	11.00	1035	12.31	1230	12.99
570	18.06	1240	12.35	1284	12.88
668	12.88	1270	12.13	1400	13.09
702	19.65	1274	12.33		
830	9.02	1300	13.05		
950	11.43	1460	13.01		
1000	19.95	1490	12.99		
1205	21.72				
1255	11.50				
1265	11.24				
1375	8.95				
1395	19.13				

+ Carbon Dioxide Exchange Rate (µmol m^{-2} s^{-1})

Table A5. Raw data for regression analysis of temperature (leaf, °C) effects on CER of Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
TEMP	CER+	TEMP	CER	TEMP	CER
9.7	24.58	5.6	6.92	10.9	13.20
11.2	18.06	8.4	8.96	11.2	9.42
11.3	21.38	8.6	5.03	11.3	6.73
11.7	23.95	10.2	7.00	12.2	15.57
13.2	25.83	13.2	6.63	13.3	15.21
14.4	27.39	14.0	9.49	14.0	19.06
14.9	27.67	14.9	8.63	14.3	11.99
17.0	18.96	18.8	9.70	14.4	18.17
20.2	25.96	19.1	6.70	14.8	17.17
20.6	27.13	19.1	5.65	15.7	14.04
22.2	27.85	19.9	5.96	16.3	9.84
22.3	22.18	22.3	6.93	16.6	10.22
25.3	22.58	23.2	7.96	22.7	13.63
25.7	21.31	24.2	7.31	22.7	11.78
26.4	21.16	24.4	4.48	23.4	15.16
27.4	22.76	26.6	5.43	25.7	8.44
29.1	22.21	29.1	5.78	28.5	10.59
29.4	20.86	31.1	4.53	28.9	8.36
30.9	23.04	30.6	4.71	29.9	9.57
31.9	18.42	31.7	4.36	31.0	8.16
32.6	22.73	34.5	2.28	31.2	10.43
32.8	17.86	35.3	0.26	31.9	11.76
33.1	18.41			32.9	12.04
33.8	21.93			33.1	7.37
36.7	19.85			35.7	7.03
37.5	9.93			37.1	0.69
37.6	18.99			37.2	5.20
38.6	15.21			37.4	7.09

+ Carbon Dioxide Exchange Rate (μmol m^{-2} s^{-1})

Table A6. Raw data for regression analysis of temperature (leaf, °C) effects on CER in the dark of Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
TEMP	CER+	TEMP	CER	TEMP	CER
8.3	3.63	6.9	0.35	9.3	1.75
8.8	1.36	8.1	0.44	9.3	0.66
9.9	1.56	8.3	0.26	9.5	0.44
10.1	1.15	10.7	0.57	10.1	1.95
14.4	1.57	13.8	1.42	15.3	2.42
14.4	4.42	14.2	1.13	15.4	3.18
15.8	3.16	16.1	0.86	15.6	2.28
16.4	4.61	23.2	7.96	16.1	1.52
21.5	1.93	24.2	7.31	16.4	1.73
21.9	8.48	24.4	4.48	16.4	0.76
22.3	7.40	25.6	4.27	16.6	2.98
22.6	5.50	25.7	5.92	22.8	2.60
26.9	9.62	26.6	5.43	22.8	5.09
27.2	9.45	27.9	3.04	23.7	1.34
27.2	8.04	28.1	3.29	24.8	7.00
30.0	5.99	30.6	5.90	30.4	4.28
30.7	3.64	30.6	4.31	31.3	10.37
31.2	3.91	32.0	2.97	32.0	8.86
31.2	6.29	32.0	2.45	32.4	2.17
33.9	7.43	35.3	7.07	35.4	2.18
34.8	8.42	35.8	8.81	32.6	3.72
39.0	9.80	35.8	5.95	33.1	8.05
		37.8	6.39	33.4	3.00
				36.3	3.92
				36.4	5.66
				38.3	12.78
				39.4	18.81

+ Carbon Dioxide Exchange Rate (μmol m^{-2} s^{-1})

Table A7. Raw data for regression analysis of ambient CO_2 concentration (L L^{-1}) effects on CER Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
CO_2	CER+	CO_2	CER	CO_2	CER
95	1.38	128	1.62	106	0.25
95	1.84	128	1.44	106	0.57
95	1.17	128	1.01	106	0.06
95	1.88	128	0.87	217	2.42
222	7.13	200	2.61	217	4.95
222	8.98	200	6.08	217	4.83
222	8.15	200	3.60	217	4.36
222	8.20	200	5.52	324	7.86
316	13.91	317	7.20	324	7.07
316	14.16	317	11.48	324	7.84
316	14.45	317	6.91	438	4.77
316	14.85	317	11.55	438	4.70
475	17.85	448	8.59	438	10.88
475	20.2	448	13.06	438	10.81
475	19.02	448	11.35		
475	18.37	448	13.96		

+ Carbon Dioxide Exchange Rate (μmol m^{-2} s^{-1})

Table A8. Data for points in graphs of PGR effects on net photosynthesis, chlorophyll content and dry/weight unit area of annual bluegrass (AB) and creeping bentgrass (CB). Data points represent % of control.

	NET PHOTOSYNTHESIS		CHLOROPHYLL				DRY WEIGHT/ UNIT AREA+++	
			LA+		DW++			
RATE Kg ha^{-1}	AB	CB	AB	CB	AB	CB	AB	CB
				----------EL-500----------				
0.00	100	100	100	100	100	100	100	100
1.12	82	99	88	119	89	117	111	113
2.24	50	96	85	98	87	71	121	164
4.56	54	86	95	139	120	145	98	106
				----------MEFLUIDIDE----------				
0.00	100	100	100	100	100	100	100	100
0.14	187	96	132	163	105	142	126	122
0.28	142	117	232	231	148	175	149	136
0.56	226	121	168	171	112	139	157	131

ANALYSIS OF VARIANCE

SOURCE	df	------------MEAN	SQUARE------------		
			---EL-500---		
REP	4	4422.79**	4317.45**	1506.66	86.06
SPECIES	1	5569.60**	4862.03**	689.81	1485.13
RATE	3	2050.43*	1100.69	3912.60*	3034.75
S X R	3	950.20	930.83	883.43	807.21
ERROR	28	722.40	459.54	928.20	1257.46
			---MEFLUIDIDE---		
REP	3	25161.25*	15429.78*	10580.95**	868.62**
SPECIES	1	24310.13	552.78	4116.18	979.03
RATE	3	7428.58	23893.03**	5169.80	3349.37*
S X R	3	5194.38	496.87	509.77	276.87
ERROR	21	6988.04	3819.09	1010.19	579.35

\+ ON LEAF AREA BASIS

++ ON DRY WEIGHT BASIS

+++ df IN AOV = 3 FOR REP AND 21 FOR ERROR

Table A9. Data for points in graphs of PGR effects on net photosynthesis and chlorophyll content of annual bluegrass (AB) and creeping bentgrass (CB). Data points represent % of control.

---MEFLUIDIDE---

NET PHOTOSYNTHESIS

DAYS AFTER TREATMENT

	4		8		16		32		64	
	AB	CB	AB	CB	AB	CB	AB	CB	AB	CB
CONTROL	100	100	100	100	100	100	100	100	100	100
0.56	56	56	52	37	147	48	105	89	97	78

CHLOROPHYLL

	4		8		16		32		64	
	AB	CB	AB	CB	AB	CB	AB	CB	AB	CB
CONTROL	100	100	100	100	100	100	100	100	100	100
0.56+	97	105	118	127	169	192	89	96	103	87

-----EL-500-----

NET PHOTOSYNTHESIS

DAYS AFTER TREATMENT

	4		8		16		32		64	
	AB	CB	AB	CB	AB	CB	AB	CB	AB	CB
CONTROL	100	100	100	100	100	100	100	100	100	100
2.24	76	75	49	80	55	29	115	137	142	118

CHLOROPHYLL

	4		8		16		32		64	
	AB	CB	AB	CB	AB	CB	AB	CB	AB	CB
CONTROL	100	100	100	100	100	100	100	100	100	100
2.24+	135	163	87	146	133	168	119	110	121	98

ANALYSIS OF VARIANCE

SOURCE	df	MEAN SQUARE				
---MEFLUIDIDE---						
NET PHOTOSYNTHESIS						
REP	3	674.25	1397.50	3623.06	1653.67	2717.73
SPECIES	1	0.00	240.25	9950.06	272.25	370.56
RATE	1	7832.25**	12544.00**	27.56	36.00	637.56
ERROR	9	341.42	1112.33	3312.73	1491.83	3464.62
CHLOROPHYLL						
REP	3	241.89	960.83	1581.73	86.06	151.23
SPECIES	1	60.06	81.00	517.56	49.00	248.06
RATE	1	5.06	2025.00	25840.56**	240.25	95.06
ERROR	9	309.01	1277.94	2002.40	268.36	180.12

Table A-9 con't

			---EL-500---			
			NET PHOTOSYNTHESIS			
REP	3	1108.06	3716.40	271.50	396.23	5782.42
SPECIES	1	1.56	976.56	676.00	517.56	600.25
RATE	1	2376.56	4935.06	13689.00**	2678.06	3540.25
ERROR	9	646.29	1528.95	637.72	1483.45	7073.31
			CHLOROPHYLL			
REP	3	4319.75	771.33	168.75	117.83	75.90
SPECIES	1	784.00	3481.00	1190.25*	81.00	564.26
RATE	1	9702.25	1024.00	10100.25**	841.00	351.56
ERROR	9	2842.92	1756.89	187.42	168.06	319.90

+ kg ha^{-1}

NOTE: RATE X SPECIES INTERACTION = MEAN SQUARE FOR SPECIES.

Table A10. Raw data for regression analysis of VPD (vapor pressure deficit) effects on CER of Kentucky bluegrass, creeping bentgrass and annual bluegrass.

KENTUCKY BLUEGRASS		CREEPING BENTGRASS		ANNUAL BLUEGRASS	
VPD	CER+	VPD	CER	VPD	CER
0.68	24.51	0.49	10.14	0.46	8.88
0.74	22.78	0.50	11.34	0.46	8.61
0.74	23.77	0.51	9.71	0.46	8.99
0.74	23.72	0.54	5.65	0.47	9.17
0.75	20.33	0.56	9.70	0.48	9.24
0.81	24.38	0.60	6.62	0.49	8.95
0.89	23.96	0.64	5.67	0.53	4.79
0.92	21.83	0.69	10.02	0.56	8.97
0.94	19.10	0.70	8.30	0.59	5.16
0.96	18.26	0.72	5.96	0.82	10.97
0.99	23.37	0.78	7.68	0.89	7.83
0.99	22.31	0.99	6.93	0.90	7.56
1.00	19.70	1.00	6.36	0.91	7.54
1.07	21.67	1.00	6.81	0.98	7.59

+ Carbon Dioxide Exchange Rate (μmol m^{-2} s^{-1})