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Carbon Dioxide Exchange Rate and Chlorophyll Content of Turfgrasses Treated with Flurprimidol or Mefluidide

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Abstract. Plant growth regulators (PGRs) are being used increasingly for high maintenance turf production. A greenhouse and growth chamber study was conducted to determine the effect of two PGRs, mefluidide and flurprimidol, on the carbon dioxide exchange rate, chlorophyll content, and specific leaf weight of annual bluegrass and creeping bentgrass. Rate-response and time course studies were conducted. In the rate-response study, increasing flurprimidol rates caused a linear decrease in the carbon dioxide exchange rate (CER). Mefluidide had no effect on the CER in the rate-response experiment but did cause a significant drop in the CER at 4 and 8 days after treatment (DAT) in the time course study. Both PGRs increased chlorophyll content at 16 DAT in the time course study. In the rate-response study, chlorophyll content displayed a quadratic response to an increasing mefluidide rate. The 0.28 kg ha^{-1} rate of mefluidide increased the chlorophyll content to 46 $\mu g\ cm^{-2}$ from 21.5 $\mu g\ cm^{-2}$ for control plants. Both PGRs increased specific leaf weight, although for flurprimidol the effect was significant only at the 0.1 level of probability. PGRs decreased the CER and increased the chlorophyll content and specific leaf weight for both species tested. The physiologic effects measured were short lived, and so the physiologic significance of these changes is difficult to determine without further research.

Key Words. *Poa annua—Agrostis palustris*—Plant growth regulators

Plant growth regulators (PGRs) can reduce significantly the costs associated with maintaining turf (Foote and Himmelman 1971). The scope of PGR use in turf ranges from vegetative and seedhead suppression of roadside grasses to mowing reduction of golf course greens mown as low as 0.3 cm. In addition, PGRs have been used in turf for weed suppression, increased ball roll, and increased stress tolerance.

When PGRs are used on high quality turf, their effects on photosynthesis, total nonstructural carbohydrates, root growth rates, and lateral stem and secondary tiller production become very important. However, limited data are available on most of these topics, and where it does exist, it is often contradictory (Breuninger and Watcshke 1989, Dernoeden 1984, Jiang and Marcum 1994). For example, Jiang and Marcum (1994) found that five different PGRs including mefluidide [*N*-(2,4-dimethyl-5-{[(trifluoromethyl)sulfonyl]amino}phenyl) acetamide] and paclobutrazol [β-{(4-chlorphenyl)-methyl}-α-(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol] reduced root growth in tall fescue (*Festuca arundinacea* Schreb.). However, Dernoeden (1984) saw an increase in root growth in Kentucky bluegrass (*Poa pratensis* L.) treated with flurprimidol [α-(1-methylethyl)-α-{4-(trifluoromethoxy)phenyl}-5-pyrimidinemethanol].

Spokas and Cooper (1991) studied the effects of mefluidide and amidochlor [*N*-({acetylamino}methyl)-2-chloro-*N*-(2,6-diethylphenyl)acetamide] on the apparent photosynthetic rate and chlorophyll content of Kentucky bluegrass. They found that mefluidide decreased the apparent photosynthesis in two of three studies conducted in a greenhouse at 13, 19, and 39 days after treatment

Abbreviations: PGR(s), plant growth regulator(s); DAT, days after treatment; CER, carbon dioxide exchange rate; GA(s), gibberellic acid(s).

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(DAT) in one study and at 15, 17, and 27 DAT in the second study. Two of four field studies on field-grown Kentucky bluegrass showed a reduction in photosynthesis by mefluidide. However, they noted that variability in these studies was quite high, and this prevented finding significance on other sampling dates. Amidochlor did not decrease the apparent photosynthesis in any of their studies when compared with a mown control. Spokas and Cooper (1991) were unable to determine whether the lack of reproducibility with mefluidide on apparent photosynthetic rates was the result of experimental variability or differences in the response of Kentucky bluegrass to different application timings or environmental conditions.

Some work on photosynthetic responses to PGRs has been conducted on other crops. Archbold and Houtz (1988) studied the effects of flurprimidol and paclobutrazol on net photosynthesis of strawberry (*Fragaria x ananassa*). No effect on net photosynthesis was observed at 3 or 12 months after PGR treatment. However, a lower level of ribulose bisphosphatase activity was measured 3 months following paclobutrazol application.

PGRs have been shown to change the growth rate of tillers, rhizomes, and roots and to inhibit seedhead development of treated turfgrasses (Breuninger and Watcshke 1989). Cooper et al. (1987) showed an increase in root elongation and rooting depth from applications of mefluidide to annual bluegrass (*Poa annua* var. reptans (Hausskn.) Timm), although the increase in rooting may be the result of a repartitioning of carbohydrates caused by seedhead inhibition by the PGR. In Kentucky bluegrass, mefluidide has been found to inhibit root and tiller production but increase rhizome length (Christians and Nau 1984, Elkins et al. 1977, Freeborg and Daniel 1981, Schmidt and Bingham 1977), whereas flurprimidol increased tiller production (Dernoeden 1984). Both mefluidide and flurprimidol have been shown to alter photosynthate partitioning in Kentucky bluegrass (Hanson and Branham 1987). Brueninger and Watschke (1989) have reviewed the effects of PGRs on turfgrass growth.

Plant growth regulators that inhibit cytochrome P-450 oxidase activity, e.g. paclobutrazol and flurprimidol, have been shown to increase palisade mesophyll cell density by up to 40% (Benton and Cobb 1995). Thus, because PGRs do alter plant morphology, it is reasonable to expect that some alterations in plant physiologic processes might also occur. From a plant management viewpoint, it is important to determine whether photosynthesis is reduced by PGR application since this could have direct bearing on plant performance during and following PGR application.

In the field, applications of furprimidol have been shown to suppress selectively the growth of annual bluegrass in mixed stands with perennial ryegrass (*Lolium perenne* L.) (Breuninger and Watcshke 1982) or creeping bentgrass (*Agrostis palustris* Huds.) (Shoop et al. 1986). To understand this selective species response to PGRs, the experiments described in this paper were conducted to determine the influence of flurprimidol and mefluidide on the carbon dioxide exchange rate (CER), chlorophyll content, and specific leaf weight of annual bluegrass and creeping bentgrass.

Materials and Methods

Plant Material and Analysis

Field-grown tillers were obtained from mature stands of annual bluegrass and creeping bentgrass 'Penncross' located at the Hancock Turfgrass Research Center, East Lansing, MI, and transplanted into 350-mL styrofoam cups. The growth medium was 5:3:1, v/v/v (sandy loam: sand:peat moss). Plants were grown in a greenhouse where temperatures fluctuated between 16 and 24°C and relative humidity between 50 and 80%. Plants were watered twice daily with an automatic misting system and fertilized with urea at a rate of 1.3 g of nitrogen m^{-2} $week^{-1}$. Supplemental lighting from metal-halide lamps provided a 16-h day length.

The CER was measured using an open gas analysis system (Augustine et al. 1976) as modified by Sams and Flore (1982). Measurements were made on 5–15 intact leaf blades placed into the assimilation chamber so that leaf-to-leaf shading was minimal. Older leaves were excluded from the chamber to ensure maximum gas exchange. Assimilation chamber conditions included an ambient temperature of 21°C, ambient CO_2 between 320 and 345 μL/liter, light intensity of >1,000 μmol m^{-2} s^{-1}, and leaf to air vapor pressure deficits ≤1.5 kPa. The CER was calculated as a molar flux using the mol fraction of CO_2 (Cowen 1977). The CER was calculated on a leaf area basis using computer programs designed by Moon and Flore (1986). Chlorophyll was extracted from fresh leaf material using *N*,*N*-dimethylformamide (Moran and Porath 1980). Samples were maintained in the dark at 4–5°C for 48 h prior to analysis on a Beckman DU spectrophotometer (Beckman Instruments, Inc., Fullerton, CA). Total chlorophyll was expressed on a leaf area basis and calculated using previously developed extinction coefficients (Inskeep and Bloom 1985). Leaf dry weight/unit of leaf area was determined 1 day prior to determination of the CER by removing five to ten leaves from each plant sample. Leaf area was determined using a Li-Cor LI-3000 leaf area meter (LI-COR Inc., Lincoln, NE). Leaves were dried in a forced air dryer at 65°C for 48 h and the dry weight recorded. Data are reported as mg dry weight/cm of leaf area.

Rate Response Studies

Plants were treated with mefluidide at 0, 0.14, 0.28 and 0.56 kg ai ha^{-1} or flurprimidol at 0, 1.1, 2.2, or 4.5 kg ha^{-1}. Treatments were applied via a conveyor belt sprayer equipped with an 8002E nozzle calibrated to deliver 770 liters ha^{-1} at a pressure of 0.21 MPa. Data described above were collected for mefluidide treatments at 10 DAT and for flurprimidol at 9 DAT. Each PGR was analyzed separately as a two species × four rate factorial with four replications.

Time Course Study

Plants were treated with mefluidide at 0 or 0.28 kg ha^{-1} or with flurprimidol at 0 or 2.2 kg ha^{-1}. Treatments were applied as described in the rate study. Data were collected on the CER and total chlorophyll

Table 1. ANOVA for the response of annual bluegrass and creeping bentgrass to varying rates of mefluidide or flurprimidol.

Source	*df*	Chl. content	Specific leaf weight	CER
		(*mean square*)		
Flurprimidol				
Block	3	138.1[a]	1.4[b]	4.7
Species	1	0.3	1.3[b]	1.9
Rate	3	48.7	0.8[c]	19.6[a]
Species × rate	3	65.8[c]	0.3	2.9
Error	21	26.8	0.3	2.7
Mefluidide				
Block	3	46.1	0.2	26.8[a]
Species	1	108.6	2.5[c]	7.5
Rate	3	828.9[a]	5.5[a]	1.2
Species × rate	3	22	0.5	4.0
Error	21	126.1	0.8	5.1

[a] Significance at 0.01 level of probability.
[b] Significance at 0.05 level.
[c] Significance at 0.1 level.

at 4, 8, 16, 32, and 64 DAT. The treatment design was a two species × two PGR factorial analyzed as a split block in time with days after treatment as the subplots. Four replications were used, and analysis of variance was performed using SuperAnova (Abacus Concepts, Berkeley, CA).

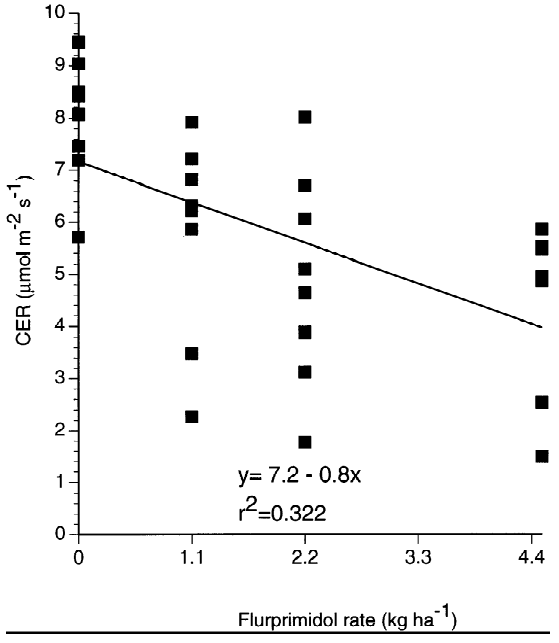

Fig. 1. Regression analysis of the effect of flurprimidol rate on the CER (μmol CO_2 m^{-2} s^{-1}) of annual bluegrass and creeping bentgrass. Each flurprimidol rate contains eight data points representing two species and four replications.

Results

Rate-Response Study

The analysis of variance for the rate-response studies of flurprimidol and mefluidide indicated significant responses in chlorophyll content, specific leaf weight, and the CER (Table 1). Increasing the flurprimidol rate caused a significant ($p = 0.01$) linear decrease in the CER (Fig. 1). The two species, however, did not differ in their CER response to flurprimidol. The analysis of variance indicated that there was no significant effect of the flurprimidol rate on the chlorophyll content (Table 1). The species differed ($p = 0.05$) in specific leaf weight with annual bluegrass having a specific leaf weight of 2.1 mg cm^{-2}, whereas creeping bentgrass had denser leaves with a specific leaf weight of 2.5 mg cm^{-2}. The effect of increasing the flurprimidol rate on specific leaf weight was significant at $p = 0.1$. Untreated grasses had a specific leaf weight of 2.1 mg cm^{-2}, whereas treatment with 1.1 or 2.2 kg ha^{-1} of flurprimidol increased specific leaf weights to 2.4 and 2.8 mg cm^{-2}, respectively. However, the 4.5 kg ha^{-1} rate caused no change in the specific leaf weight when compared with the untreated plants.

Mefluidide had no effect on the CER (Table 1). However, both the chlorophyll content and specific leaf weight responded to mefluidide treatment. Mefluidide caused an increase ($p = 0.01$) in specific leaf weight with an increasing rate of application (Fig. 2). The analysis of variance showed this response to have significant linear and quadratic components. The response appears linear at the lower end of the rate range, but it levels out as rates are increased above 0.28 kg ha^{-1}. The effect of mefluidide on the chlorophyll content displayed a sig-

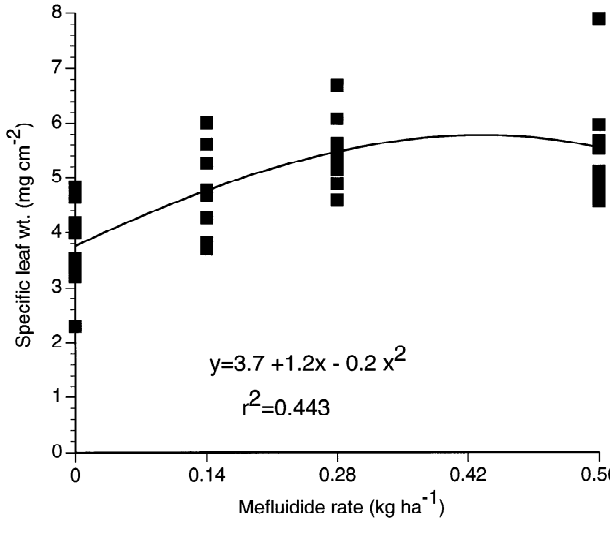

Fig. 2. Regression analysis of the effect of mefluidide rate on the specific leaf weight (mg dry weight cm^{-2} leaf area) of annual bluegrass and creeping bentgrass. Each mefluidide rate contains eight data points representing two species and four replications.

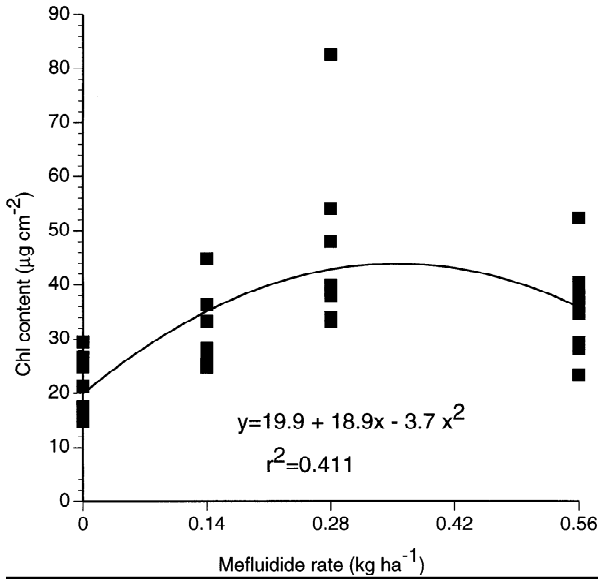

Fig. 3. Regression analysis of the effect of mefluidide rate on the chlorophyll content (μg cm^{-2}) of annual bluegrass and creeping bentgrass. Each mefluidide rate contains eight data points representing two species and four replications.

nificant quadratic response (Fig. 3). Chlorophyll content increased from 21.5 μg cm^{-2} for the untreated plants to 46.0 μg cm^{-2} for those plants receiving 0.28 kg ha^{-1} mefluidide.

Time Course Study

The analysis of variance showed significant main effects on the CER due to day of measurement, PGR treatment, and interactions of species × day and PGR × day (Table 2). The two species did not differ in their CER response to PGR treatment. Both PGRs suppressed the CER at 4 and 8 DAT, and flurprimidol continued to suppress the CER at the 16 DAT measurement (Table 3). No further differences in the CER were observed at 32 or 64 DAT. When averaged over observation dates and species, treatment with mefluidide reduced the CER to 10.1 μmol m^{-2} s^{-1}, whereas flurprimidol treatment reduced the CER to 11.1 μmol m^{-2} s^{-1} compared with a value of 16.6 μmol m^{-2} s^{-1} for untreated plants.

The effect of PGRs on the chlorophyll content was expressed as significant PGR × day interaction, and significant species, PGR, and day of treatment main effects (Table 2). The chlorophyll content was increased at 16 DAT by both PGRs (Table 4). At 32 DAT, neither PGR differed from the control; however, treatment with flurprimidol produced plants with higher chlorophyll contents than mefluidide-treated plants. The significant species difference was independent of PGR treatment, indicating that creeping bentgrass (47.6 μg cm^{-2}) had a naturally higher chlorophyll content than did annual bluegrass (42.1 μg cm^{-2}).

Table 2. ANOVA for the time course response of annual bluegrass and creeping bentgrass to mefluidide at 0.28 kg ai ha^{-1} or flurprimidol at 2.2 kg ai ha^{-1}.

Source	*df*	CER	Chl content
		(*mean square*)	
Day	4	1120.1[a]	2040[b]
Error a	12	127.45	313.1
Block	3	222.8[c]	137.1
Species	1	39.9	908.9[a]
PGR	2	490.3[b]	680.9[a]
Species × PGR	2	136.9	14.7
Species × day	4	239.5[a]	115.4
PGR × day	8	170.3[a]	425.1[b]
PGR × species × day	8	56.0	69.4
Error b	75	58.2	114.0

[a] Significance at 0.01 level of probability.
[b] Significance at 0.001 level.
[c] Significance at 0.05 level.

Table 3. CER of turfgrasses treated with mefluidide at 0.28 kg ai ha^{-1} or flurprimidol at 2.2 kg ai ha^{-1} and measured at five dates after application. Data are expressed as μmol of CO_2 m^{-2} s^{-1} and are the mean of both grass species.

	Days after treatment				
Treatment	4	8	16	32	64
Control	34.7[a] a	7.1 a	12.0 a	14.8	14.3
Mefluidide	15.4 b	3.2 b	11.1 ab	13.6	7.2
Flurprimidol	18.0 b	3.9 ab	4.8 b	17.7	10.8
Significance	*	†	†	N.S.	N.S.

[a] Means followed by different letters are significantly different as determined by Fisher's protected LSD at the 0.1 or 0.05 level of probability, † or *, respectively.

Discussion

The time course and rate response studies taken together indicate that both compounds inhibit the CER but that the effect of mefluidide is of shorter duration than that observed with flurprimidol. In the rate study, data on the mefluidide rate response were collected at 10 DAT and indicated that there was no effect upon the CER. In the time course study, mefluidide inhibited the CER at 4 and 8 DAT. By 16 DAT, the mefluidide CER had returned to the level of the control. Therefore, the period of CER inhibition by mefluidide was too short to be detected in the rate-response study where the CER was measured at 10 DAT. The difference in length of the CER inhibition might be explained by a shorter uptake period for me-

Table 4. Chlorophyll content of turfgrasses treated with mefluide at 0.28 kg ai ha^{-1} or flurprimidol at 2.2 kg ai ha^{-1} and measured at five dates after application. Data are expressed as μg of chlorophyll cm^{-2} leaf area and are the mean of both grass species.

	Days after treatment				
Treatment	4	8	16	32	64
Control	39.1[a]	32.1	32.9 a	59.7 ab	40.2
Mefluidide	37.2	39.1	58 b	52.9 b	36.5
Flurprimidol	52.6	35.9	49 b	66.5 a	40.9
Significance	N.S.	N.S.	***	*	N.S.

[a] Means followed by different letters are significantly different as determined by Fisher's protected LSD at the 0.05 or 0.001 levels of probability, *, or ***, respectively.

fluidide as a foliar absorbed material (Field and Whitford 1982) vs the root uptake of flurprimidol. Root uptake would be more continuous and controlled by the half-life of flurprimidol in soil. Foliar absorption of mefluidide would have a defined, shortened window for uptake to occur on a turf receiving irrigation and mowing.

In contrast to mefluidide, flurprimidol-treated grass showed a significant linear decrease in the CER with increasing dose when measured at 9 DAT (Fig. 1). In the time course study, grass CER was depressed by flurprimidol at 4 DAT ($p = 0.05$) and was also depressed at 8 and 16 DAT ($p = 0.1$). Thus both the time course and rate-response studies demonstrate a consistent effect of a reduced CER due to flurprimidol.

Several authors (Arteca and Dong 1981, Davies 1987, Karnok and Beard 1983) support the hypothesis that gibberellic acids (GAs) act as photosynthesis promoters. Data from Archbold and Houtz (1988), Spokas and Cooper (1991), and the data presented here indicate that PGRs that inhibit GA biosynthesis have a moderate inhibitory effect on the CER, possibly by reducing endogenous levels of GA.

Grass chlorophyll content displayed a quadratic response to an increasing mefluidide rate, with a linear increase in the chlorophyll content as the mefluidide rate was increased to 0.28 kg ha^{-1}. Treatment with flurprimidol did not affect the chlorophyll content in the rate-response study. In the time course study, both mefluidide and flurprimidol increased plant levels of chlorophyll at 16 DAT compared with the control. At 32 DAT, flurprimidol-treated turf had a significantly higher level of chlorophyll than did mefluidide-treated turf, whereas neither PGR altered the chlorophyll content compared with the control. The two studies together indicate that mefluidide increases chlorophyll content sooner after application than does flurprimidol. However, the response to flurprimidol may last longer, as indicated by the data from the time course study.

Spokas and Cooper (1991) saw an increase in the chlorophyll content at 7 DAT but not at 6 or 8 DAT in their study of the Kentucky bluegrass response to mefluidide treatment. The increase in visual turf quality seen from PGR applications seems to last longer than what this study or that of Spokas and Cooper (1991) indicates from increased chlorophyll content.

None of the data presented indicated a differential response to PGRs by annual bluegrass or creeping bentgrass. The basis of the selective suppression of annual bluegrass by flurprimidol does not appear to be caused by a selective reduction in the CER.

Both PGRs increased specific leaf weight of both species. Other GA-inhibiting compounds, particularly the triazole class of fungicides and PGRs, have been shown to increase specific leaf weight (Benton and Cobb 1995).

The data presented show that CER is clearly reduced by treatment with mefluidide or flurprimidol for at least the first 16 DAT. The reduction in the CER may be correlated to a reduction in endogenous levels of GA. There was no indication of an increase in CER after the period of growth inhibition, which may be expected if endogenous GA levels rebound following suppression. Mefluidide significantly increased both the chlorophyll content and specific leaf weight, whereas flurprimidol increased the specific leaf weight ($p = 0.1$). Flurprimidol increased the chlorophyll content but only at 16 DAT in the time course study. The flurprimidol rate-response study, conducted at 9 DAT, did not show a significant increase in chlorophyll from flurprimidol applications.

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