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A Putative Prodiamine-Resistant Annual Bluegrass (*Poa annua*) Population is Controlled by Indaziflam

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Prodiamine is a mitotic inhibiting herbicide regularly used to control annual bluegrass PRE. A population of annual bluegrass not controlled by prodiamine at 1,120 g a.i. ha^{-1} was identified on a golf course in Alcoa, TN, in 2012. A whole-plant hydroponics bioassay was used to screen this biotype for prodiamine resistance (PR) compared with a known susceptible population (SS). Multitiller (i.e., > 4 tillers) PR and SS annual bluegrass plants were established in hydroponic culture and exposed to 0, 0.001, 0.01, 0.10, 1.0, and 10.0 mM prodiamine. Exposure to prodiamine at 0.001 mM reduced root growth of the SS biotype to 26% of the nontreated check (i.e., 0 mM prodiamine) but had no effect on the PR biotype. When exposed to 10 mM prodiamine, root growth of the PR biotype was reduced to 24% of the nontreated check compared with 9% for the SS biotype. I_{50} values for the PR and SS biotypes were 0.04 and 2.8×10^{-6} mM prodiamine, respectively. The PR biotype measured lower in plant height and leaf width than the SS population. In field trials, prodiamine at 560, 840, 1,120, and 1,400 g ha^{-1} only controlled the PR biotype 0 to 22%. PRE applications of the cellulose biosynthesis inhibitor indaziflam at 35, 52.5, and 70 g a.i. ha^{-1} controlled this PR biotype 70 to 97%. This marks the second instance of annual bluegrass developing resistance to prodiamine in Tennessee during the past 5 yr. Future research should evaluate indaziflam efficacy for control of other prodiamine-resistant biotypes of annual bluegrass as well as annual bluegrass biotypes resistant to herbicidal inhibitors of 5-enolpyruvylshikimic acid-3-phosphate synthase, acetolactate synthase, and photosystem II.

Nomenclature: Indaziflam; prodiamine; annual bluegrass, *Poa annua* L. var. *annua*; bermudagrass, *Cynodon dactylon* L. Pers.

Key words: Cellulose; cellulose biosynthesis inhibitor, dinitroaniline, golf course, herbicide resistance, mitotic inhibitor, turf, turfgrass.

Annual bluegrass is a problematic winter annual turfgrass weed. Annual bluegrass infestations in warm-season turfgrass, commonly occurring during periods of winter dormancy, can negatively affect aesthetic and functional turfgrass quality (Toler et al. 2007). Herbicide resistance in annual bluegrass is particularly concerning given that this species has developed resistance to nine different sites of action (Heap 2013). Additionally, > 75% of the instances of herbicide resistance that have been documented in turfgrass situations have occurred in annual bluegrass (Heap 2013).

Prodiamine is a dinitroaniline herbicide that disrupts mitosis in susceptible plants by preventing the protein tubulin from polymerizing to form microtubules required for cell division (Vaughn and Lehnen 1991). Without microtubules, the spindle apparatus is unable to form during mitosis, and sister chromatids are not able to segregate during anaphase; thus, cell division is halted (Anthony and Hussey 1999). Annual bluegrass can be effectively controlled with PRE applications of prodiamine in late summer (Dernoeden 1998). Widespread use of prodiamine for PRE annual bluegrass control has led to the development of prodiamine-resistant biotypes of annual bluegrass in the southeastern United States. Isgrigg et al. (2002) documented the presence of a prodiamine-resistant annual bluegrass biotype on a golf course fairway in Charlotte, NC, after eight consecutive years of dinitroaniline herbicide applications. In shoot and root growth dose–response experiments, this resistant biotype from North Carolina exhibited 6- to 105-fold resistance to prodiamine compared with a known susceptible biotype. Similarly, Cutulle et al. (2009) used hydroponic methodology to confirm the presence of a prodiamine-resistant annual bluegrass biotype in Chattanooga, TN. This biotype required 26 times more prodiamine to reduce root growth by 50% compared with a susceptible biotype.

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Unlike dinitroaniline herbicides, multiple sites can be inhibited by cellulose biosynthesis–inhibiting herbicides to control weeds (Barbham and Debolt 2013; Sabba and Vaughn 1999). To date, there are no instances of weed resistance to cellulose biosynthesis–inhibiting herbicides other than quinclorac (Heap 2013). However, it should be noted that data directly suggest that quinclorac does not inhibit cellulose biosynthesis in monocots (Tresch and Grossmann 2003). Indaziflam is an alkylazine cellulose biosynthesis–inhibiting herbicide with excellent efficacy for PRE and early POST annual bluegrass control at rates of 30 to 60 g ha^{-1} (Brosnan et al. 2012; Meyers et al. 2009; Perry et al. 2011). Indaziflam applications, alone or in rotation with other modes of action, may provide turfgrass managers with an option for managing herbicide resistance in annual bluegrass.

In the spring of 2012, poor annual bluegrass control ($< 50\%$) was reported on golf course roughs in Alcoa, TN, after prodiamine treatment at 1,120 g ha^{-1} the previous year. Prodiamine had been exclusively applied in this manner for residual weed control for > 10 yr consecutively at this location (JD Murr, personal communication). Should this biotype be resistant to prodiamine, it would mark the second occurrence of annual bluegrass developing resistance to prodiamine in Tennessee during the past 5 yr. Thus, the objective of this research was to determine the sensitivity of a putative prodiamine-resistant annual bluegrass biotype collected from this location. A second objective was to determine whether PRE applications of indaziflam could control this biotype in the field.

Materials and Methods

Greenhouse Studies Confirming Resistance. Mature annual bluegrass plants suspected to be resistant to prodiamine (hereafter referred to as PR) were harvested from bermudagrass roughs at Lambert Acres Golf Club (Alcoa, TN; 35.747307°N, 83.8840667°W) during January 2013. These plants had not been treated with any herbicide in the fall of 2012. A biotype known to be susceptible to prodiamine (hereafter referred to as SS) was harvested in the same manner from a location 25 km from Lambert Acres Golf Club at the East Tennessee Research and Education Center (Knoxville, TN). Annual bluegrass is a self-pollinated species (Ellis 1973), and because seed was limited, individual tillers of the PR and SS biotypes were removed from plants harvested in the field and transplanted into 164-cm^3 conetainers (SC10 Super Cell Conetainer, Steuwe & Sons, Tangent, OR 97389) filled with a peat moss growing medium (Growing Mix no. 2, Conrad Fafard Inc., Agawam, MA 01001). All tillers were transplanted from each of the 100 PR and SS plants harvested, thus producing 490 single-tiller PR and SS transplants for use in greenhouse experiments. These transplants were maintained under controlled greenhouse conditions for a minimum of 2 wk before initiating research. During the 2-wk acclimation period, plants were irrigated to prevent the onset of wilt and clipped daily at a height of ~ 5 cm. Plants were fertilized with a complete fertilizer (20–8.7–16.6 N–P–K; Howard Johnson's Triple Twenty Plus Minors, Milwaukee, WI) at 24.5 kg N ha^{-1}. Average daily maximum/minimum temperatures in the greenhouse measured 27/19 C under conditions of natural light. By the time greenhouse experiments were initiated these transplants had matured such that all plants had a minimum of four tillers.

Sensitivity of the PR and SS biotypes to prodiamine was confirmed using methods similar to Cutulle et al. (2009) in a greenhouse at the University of Tennessee (Knoxville, TN; 35.95°N). This method was selected in that it has been found to be the fastest method of detecting annual bluegrass resistance to dinitroaniline herbicides (Cutulle et al. 2009). Polyethylene containers (Rubbermaid Roughneck, Rubbermaid Commercial Products LLC, Winchester, VA) were filled with 10 L of a full-strength Hoagland solution (Hoagland and Arnon 1950) and aerated with a blower (Model VB-007S, Sweetwater, Ft. Collins, CO) connected to air stones (HAGEN Elite 1″ Cube Air Stone, Rolf C. Hagen Corp., Mansfield, MA) in each container (Kopsell et al. 2007). Tygon tubing (Saint-Gobain Performance Plastics, Akron, OH) was used to connect the blower to the air stones in each container. Deionized water was added as needed to maintain a 10-L volume in each container. Ten holes (0.4 mm diam) were drilled into the lid of each container, spaced 5.3 mm apart. Annual bluegrass plants in each container were washed free of soil and inserted into each hole such that root tissues were submerged in the nutrient solution. Thus, mean values for a single container were generated using 10 subsamples. Plants were not mowed (i.e., clipped) after transplanting. During both experimental runs, day/night temperatures in the greenhouse were set to 26/21 C. Average daily solar radiation during the first and second experimental runs ranged from 1.4 to 348 W m^{-2} and 1.4 to 455 W m^{-2}, respectively.

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Table 1. Morphological characteristics of prodiamine-resistant (PR) and susceptible (SS) annual bluegrass harvested in Alcoa and Knoxville, TN, respectively in 2013. Data collected on nontreated check plants in two experiments conducted in hydroponic culture.

Biotype	Tiller no.	Plant height	Leaf width
		cm	mm
PR	4.7	5.7	2.4
SS	5.6	6.8	3.7
$P > T_{0.05}$	NS[a]	**	***

[a] Abbreviation: NS, not significant.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

After a 5-d acclimation period, aboveground morphological data were collected to describe the PR and SS biotypes. Tiller number, plant height, and leaf width were measured on nontreated PR and SS plants, with means compared by *t* test at the $\alpha = 0.05$ level (Table 1). Additionally, roots of both PR and SS plants were trimmed to a uniform length of 6 cm to facilitate assessments of root growth in response to herbicide treatment. Similar to Cutulle et al. (2009), PR and SS plants were exposed to 0, 0.001, 0.01, 0.1, 1.0, and 10 mM prodiamine (Barricade 65 WG, Syngenta Professional Products, Greensboro, NC). At 10 d after herbicide treatment (DAT), root length was measured on each plant in the container. Root length data were used to determine effects of prodiamine concentration on root growth (as a percentage of the nontreated check) using the equation:

$$\text{Root growth}(\%) = \left[\left(\text{Root length}_{10\ \text{DAT}} - 6\text{–cm trimming length}\right) \Big/ \left(\text{Root length}_{\text{nontreated at 10 DAT}} - 6\text{–cm trimming length}\right)\right] \times 100 \quad [1]$$

Experiments were arranged in a randomized complete block design with three replications and repeated in time during 2013. All data were subjected to ANOVA in SAS (SAS version 9.1, SAS Institute, Cary, NC). No significant experimental run interactions were detected; therefore, data from each experimental run were combined. Log-logistic regression analysis was conducted to evaluate PR and SS responses to prodiamine using the model proposed by Seefeldt et al. (1995),

$$y = C + \left\{(D - C) \Big/ \left[1 + (x/I_{50})^{b}\right]\right\} \quad [2]$$

where y is annual bluegrass response (i.e., root length, root biomass), x is prodiamine concentration (mM), D is the upper limit for y, C is the lower limit for y, I_{50} is concentration of prodiamine giving a 50% response (i.e., 50% reduction in root growth), and b is the slope of the line at I_{50}. All regression analyses were conducted using Prism software (Prism 5.0 for Mac OS X, GraphPad Software, La Jolla, CA)

Field Experiments Evaluating Alternative Control Options. Field experiments were conducted at Lambert Acres Golf Course evaluating the efficacy of indaziflam for PRE control of a prodiamine-resistant annual bluegrass biotype. Trials were conducted on two golf course roughs located ~ 600 m from one another. A decision was made to replicate the trials spatially because the golf course superintendent desired to eradicate the population expeditiously; thus, replication over subsequent years was not possible. Soil at each trial location was a Dewey silty clay loam (fine, kaolinitic, thermic typic Paleudults). Turf in each location was hybrid bermudagrass (*C. dactylon* × *C. transvaalensis* Burtt-Davey) mowed once weekly at 4.5 cm with a reel mower. Neither site received supplemental irrigation aside from rainfall, nor was supplemental nutrition applied at either location. Turf had been treated with prodiamine at 1,120 g ha^{-1} 10 yr consecutively before initiating research. However, no herbicide applications had been made at either location in the 8 mo before initiating these studies.

Herbicide treatments included indaziflam (Specticle 20WP, Bayer Environmental Sciences, Research Triangle Park, NC) at 35, 52.5, and 70 g ha^{-1} and prodiamine at 560, 840, 1,120, and 1,400 g ha^{-1}. A nontreated check was included for comparison. All treatments were applied PRE to 1.5 × 3.0 m plots using with a CO_2-powered boom sprayer calibrated to deliver 281 L ha^{-1} using 8002 flat-fan nozzles (Teejet flat-fan spray nozzles, Wheaton, IL). Applications at each location were made on August 22, 2012. The site received approximately 1.5 cm of rainfall during the 10 d after herbicide application.

Annual bluegrass control was visually assessed using a 0% (i.e., no control) to 100% (i.e., complete control) relative to the nontreated check at 153 and 180 DAT. Annual bluegrass plant counts were also made to confirm quantitatively visual ratings of annual bluegrass control. The number of annual bluegrass plants present in two 0.1-m^2 boxes placed in the center of each plot was recorded 194 DAT.

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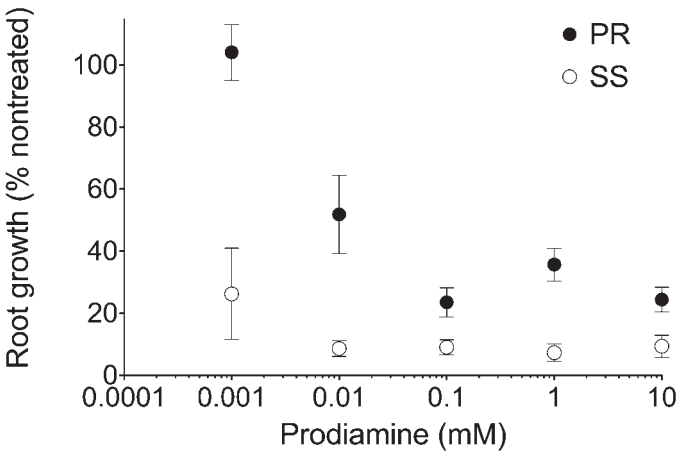

Figure 1. Root growth of prodiamine-resistant (PR) and susceptible (SS) annual bluegrass plotted as a percentage of a nontreated check (0 mM prodiamine) after exposure to increasing concentrations of prodiamine in hydroponic culture during greenhouse experiments at the University of Tennessee (Knoxville, TN) in 2013. Standard error bars are presented as a means of statistical comparison.

Experimental design at each location was a randomized complete block with three replications. Visual assessments of annual bluegrass control were arcsine transformed before being subjected to ANOVA in SAS using the expected means squares of McIntosh (1983). Interpretations of transformed data were not different from nontransformed data; therefore, nontransformed data are presented. No treatment by location interactions were detected, allowing data from each location to be combined. Fisher's protected least significant difference (LSD) test was used to separate treatment means at $\alpha = 0.05$.

Results and Discussion

Greenhouse Studies Confirming Resistance. Root growth of the PR and SS biotypes varied in response to increasing concentrations of prodiamine (Figures 1 and 2, Table 2). Exposure to prodiamine at 0.001 mM reduced root growth of the SS biotype to 26% of the nontreated check (i.e., 0.000 mM prodiamine) but had no effect on the PR biotype. When exposed to 10 mM prodiamine, root growth of the PR biotype was reduced to 24% of the nontreated check compared with 9% for the SS biotype. Using log-logistic regression, I_{50} values for the PR and SS biotypes were 0.04 and 2.8×10^{-6} mM prodiamine, respectively. This level of resistance to prodiamine in annual bluegrass is greater than previous reports (Cutulle et al. 2009; Isgrigg et al. 2002).

Compared with the SS population, PR plants measured lower in plant height and leaf width than the SS biotype (Table 1). This response could potentially be due to a fitness penalty within the PR biotype. However, the mechanism conferring resistance to prodiamine cannot be determined from these data. Moreover, morphological differences in PR and SS plants in these studies could also be a function of plants being harvested from different fields that may have contained variable growing environments. That being said, a Thr_{239}-to-Ileu mutation on the α2-tubulin gene that has been shown to confer resistance to DNA herbicides in foxtail (*Setaria viridis* × *Setaria italica*) will reduce plant growth by reducing rates of leaf emission and stem elongation (Darmency et al. 2011). Anthony and Hussey (1999) suggested that this Thr_{239}-to-Ileu mutation could stabilize microtubules during cell division, which could consequently slow rates of leaf emergence and stem elongation. Darmency et al. (2011) reported a lower plant height in DNA-resistant foxtail plants with a Thr_{239}-to-Ileu mutation in both greenhouse and field experiments; however, this mutation did not affect germination of DNA-resistant foxtail in the field.

Field Experiments Evaluating Alternative Control Options. Prodiamine failed to provide effective annual bluegrass control in the field, supporting conclusions of our greenhouse studies that the PR biotype is resistant to prodiamine (Table 3). Prodiamine applications from 500 to 1,400 g ha^{-1} only controlled the PR biotype 0 to 22% over the course of these studies. Comparatively, applications of the cellulose biosynthesis–inhibiting herbicide indaziflam controlled this PR biotype 71 to 97% by 180 DAT. Similarly, annual bluegrass plant counts on prodiamine-treated plots were greater than or equal to the nontreated check by the end of the study. Indaziflam applications at 52.5 and 70 g ha^{-1} reduced annual bluegrass plant counts compared with the nontreated check.

Our results indicate the presence of a prodiamine-resistant annual bluegrass biotype, which marks the second report of annual bluegrass resistance to prodiamine in Tennessee during the past 5 yr. Considering that annual bluegrass is self-pollinated, transfer of resistance traits through pollen dispersal is not likely because of limited gene flow (Ellis 1973; Sweeney and Danneberger 1995). Resistance at this location likely developed after repeated use of prodiamine for residual weed control, similar to what has been reported elsewhere (Isgrigg et al. 2002).

A Thr_{239}-to-Ileu substitution on the α2-tubulin gene can confer resistance to DNA herbicides such as

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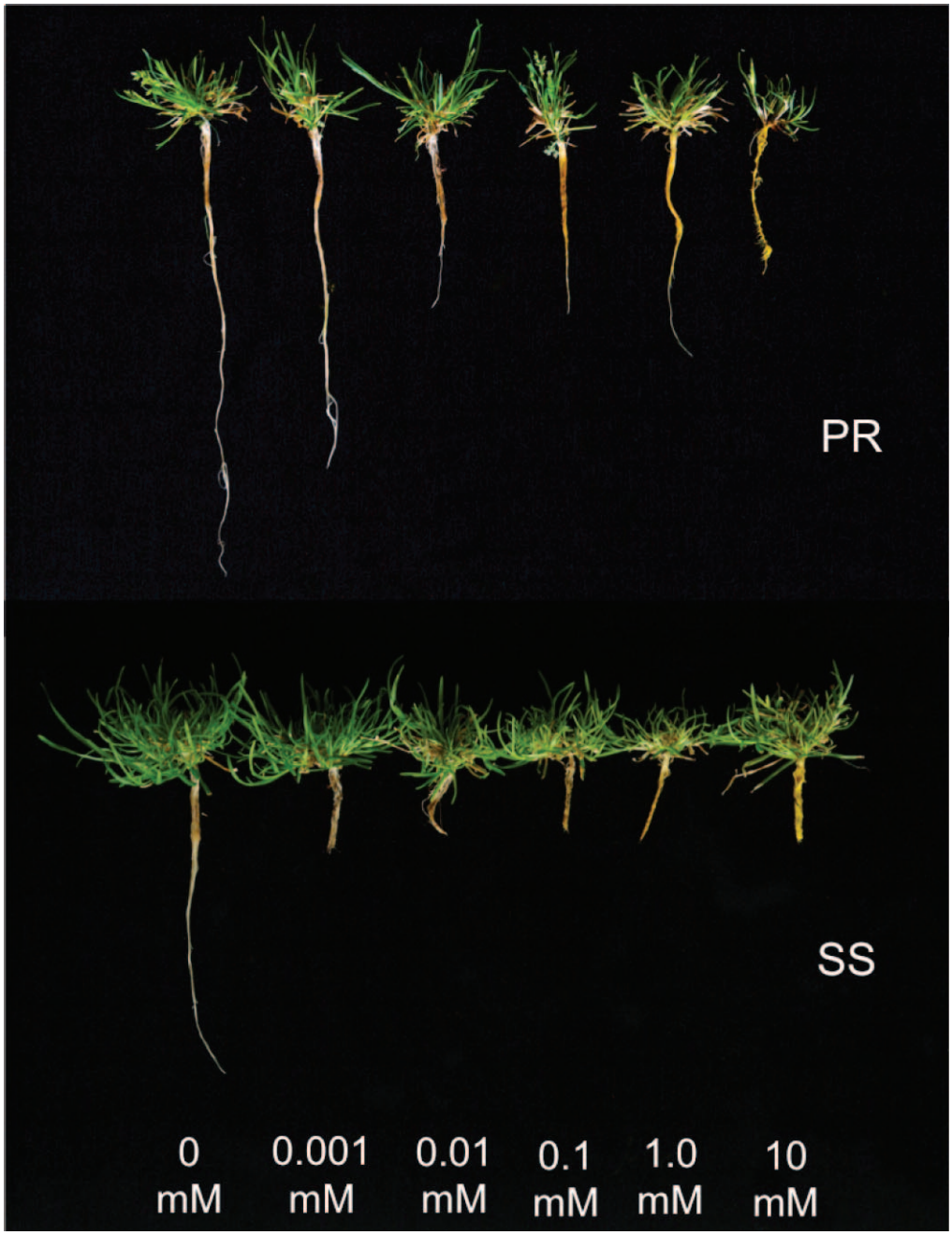

Figure 2. Prodiamine-resistant (PR) and susceptible (SS) annual bluegrass after exposure to increasing concentrations of prodiamine in hydroponic culture during greenhouse experiments at the University of Tennessee (Knoxville, TN) in 2013.

Table 2. Log-logistic regression parameters describing prodiamine-resistant (PR) and susceptible (SS) annual bluegrass root growth after exposure to increasing concentrations of prodiamine in hydroponic culture during greenhouse experiments at the University of Tennessee (Knoxville, TN) in 2013.

Biotype	I_{50}[a]	95% confidence interval	b[b]	95% confidence interval
	mM			
PR	0.043	0.012–0.161	−0.37	−0.57 to −0.18
SS	2.8×10^{-6}	2.4×10^{-10} to 0.033	−0.21	−0.45 to 0.03

[a] I_{50} is concentration of prodiamine giving a 50% reduction in root growth.
[b] b is the slope of the regression line at the I_{50} value.

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Table 3. Efficacy of PRE applications of prodiamine and indaziflam for control of a prodiamine-resistant annual bluegrass biotype located in a golf course rough in Alcoa, TN, in 2012.

Herbicide	Rate	Annual bluegrass control[a]		Plant count[c]
		153 DAT[b]	180 DAT	
	g ha^{-1}	%		No. (0.1 m^2)$^{-1}$
Prodiamine	560	7 c[d]	3 c	6 ab
	840	0 c	0 c	5 ab
	1,120	8 c	5 c	7 a
	1,400	22 c	13 c	7 a
Indaziflam	35	63 b	71 b	3 bcd
	52.5	88 a	88 a	1 cd
	70	97 a	97 a	0 d
Nontreated check	—	—	—	5 abc

[a] Annual bluegrass control was visually assessed using 0% (no control) to 100% (complete control) relative to the nontreated check.
[b] Abbreviation: DAT, days after treatment.
[c] The number of annual bluegrass plants present in two 0.1-m^2 boxes placed in the center of each plot was recorded 194 DAT.
[d] Means followed by the same letter are not significantly different from one another according to Fisher's protected LSD test at the $\alpha = 0.05$ level.

prodiamine (Darmency et al. 2011). It cannot be determined from these data whether this mutation is present in the PR biotype in this study. However, the PR biotype exhibited reduced plant height and leaf width compared with a known susceptible population, a response similar to that reported in DNA-resistant foxtail species with this Thr_{239}-to-Ileu mutation (Darmency et al. 2011). Future research should explore the molecular basis of resistance in this PR biotype and track the inheritance of this trait.

Indaziflam is a highly efficacious herbicide for selective annual bluegrass control in turf (Brosnan et al. 2012). PRE applications of indaziflam provided effective control of prodiamine-resistant annual bluegrass in this study. This response should be confirmed on other known populations of annual bluegrass resistant to prodiamine (Heap 2013). Considering that > 75% of the documented instances of herbicide resistance in turfgrass have developed in annual bluegrass, indaziflam may be an important tool for managing herbicide resistance in turf. Future research should evaluate indaziflam efficacy for control of annual bluegrass biotypes resistant to herbicidal inhibitors of 5-enolpyruvyl-shikimic acid-3-phosphate synthase, acetolactate synthase, and photosystem II.

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