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Influence of Nutrient Supply and Plant Growth Regulators on Phytotoxicity of Imazamethabenz in Wild Oat (*Avena fatua* L.)

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Abstract. The influences of nutrient supply and plant growth regulators on the phytotoxicity of imazamethabenz in wild oat (*Avena fatua* L.) were evaluated in the greenhouse. Wild oat plants supplied with half-strength rather than one-eighth-strength Hoagland solution were more susceptible to imazamethabenz, showing greater growth reduction in main shoot and tillers. The improved herbicide efficacy at higher nutrient levels appeared related to increased herbicide interception by the greater leaf surface available. Leaves developing at either nutrient level did not differ significantly in epicuticular wax, so differential absorption appeared unlikely. Wild oat plants supplemented with nutrient, switching from low to high levels at the time of herbicide application, were as susceptible to imazamethabenz or even more so than plants growing with a constant high level of nutrition. The wild oat pure-line Montana 73, a strongly tillering line, was more susceptible to imazamethabenz than the limited-tillering line, Crop Science 40. Both 2,4-D and GA_3 reduced imazamethabenz-induced tillering. Imazamethabenz efficacy was increased by GA_3 but not by 2,4-D. These results support the hypothesis that lowering apical dominance of wild oat increases imazamethabenz activity in tillers, and that increased tillering following sublethal doses of imazamethabenz treatment is associated with the release of apical dominance.

Imazamethabenz ((±)-2-[4,5-dihydro-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-4(and 5)-methylbenzoic acid (3:2)) is a selective postemergent herbicide for control of wild oat and several other weeds in cereal crops (Shaner et al. 1982). [^{14}C]-Imazamethabenz translocation from the treated wild oat leaf was largely to the main stem apex, and little radioactivity was detected in tillers (Chao et al. 1994, Smith and Chow 1990). Application of sublethal doses (100–200 g/ha) of imazamethabenz greatly inhibited wild oat main shoot growth but resulted in prolific tillering (Chao et al. 1993).

We hypothesized that the limitation in translocation of imazamethabenz to tillers was controlled by apical dominance and that enhanced tillering following imazamethabenz treatment was associated with the release of apical dominance (Chao et al. 1993). Lowering or removing apical dominance before imazamethabenz application should increase the herbicide activity in tillers, whereas maintaining apical dominance after herbicide application should inhibit imazamethabenz-induced tillering. Loss of apical dominance through destruction of the main shoot apex resulted in a threefold increase of imazamethabenz translocated to wild oat tillers, and subsequently a greater reduction in tiller growth was obtained (Chao et al. 1994).

Nutrient availability influences plant apical dominance. Increasing nutrient supply can decrease apical dominance, activate inhibited tiller buds, and promote tiller growth (Fletcher and Dale 1974, McIntyre 1990, Woodward and Marshall 1988). This should increase herbicide activity in tillers. There are several reports that improving the nutrient status of target plants increases herbicide phytotoxicity (Andrews et al. 1989, Dickson et al. 1990, McIntyre and Hsiao 1982, Nalewaja and Woznica 1985). The effect of nutrient supply on the phytotoxicity of imazamethabenz in wild oat has not been established.

Numerous genetically pure lines of wild oat exist (Naylor and Jana 1976). The different tillering capacity of each line reflects its degree of apical dominance. Under our growth conditions, pure-line

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Montana 73 (MON 73) tillered much more extensively than did pure line Crop Science 40 (CS 40) (Chao 1993). We proposed that MON 73, with its high tillering capacity and lower apical dominance, should be more susceptible to imazamethabenz than CS 40. Supporting this supposition is the report of Somody et al. (1984) that different biotypes of *Avena fatua* and *A. sterilis* showed different responses to herbicides. Biotypes tolerant to difenzoquat (1,2-dimethyl-3,5-diphenyl-1*H*-pyrazolium), MSMA (monosodium salt of methylarsonic acid), flamprop (*N*-benzoyl-*N*-(3-chloro-4-fluorophenyl)-DL-alanine), and diclofop ((±)-2-[4-(2,4-dichlorophenoxy)phenoxy]propanoic acid) tillered less than susceptible biotypes.

Plant growth regulators can modify apical dominance and influence plant tillering. Application of auxin to the destroyed main stem reversed the stimulation in tillering induced by apex destruction (Leopold 1949). The auxinlike herbicide 2,4-D [(2,4-dichlorophenoxy)acetic acid] applied to decapitated plants maintained apical dominance (Brown et al. 1979, Rood 1985). Application of exogenous gibberellic acid (GA_3) inhibited tillering in many plants (e.g., Evans et al. 1964, Sharif and Dale 1980). In addition, 2,4-D and GA_3 influence the phytotoxicity of certain herbicides (Dickson et al. 1990, Johnson and Murphy 1991). Whether 2,4-D and GA_3 could reverse the release of apical dominance due to imazamethabenz treatment and thereby reduce herbicide-induced tillering was not known at the time of this study.

The objectives of this study were 1) to determine the influence of nutrient supply on the phytotoxicity of imazamethabenz; 2) to determine whether pure line MON 73 with higher tillering capacity is more susceptible to imazamethabenz than CS 40, a limited tillering line; and 3) to determine the influence of 2,4-D or GA_3 applied after imazamethabenz treatment on the activity of this herbicide in wild oat.

Materials and Methods

Plant Growth and Imazamethabenz Application

A genetically pure line of *Avena fatua* L., CS 40, was used for all experiments except when otherwise specified. After-ripened seeds were germinated on moist filter paper at room temperature for 4 days. Five germinated seedlings with the radicles just emerging were planted to a depth of 2 cm in each 12.5-cm diameter plastic pot containing sandy loam soil in all cases except in the experiment of the influence of nutrient supply on imazamethabenz phytotoxicity. In that case, a peat moss/sand mix (3:1, v/v) was used. At the one-leaf stage all plants were thinned to 3/pot, and the plants were fertilized once with 50 ml of 20:20:20 N:P:K per pot at 3 g/L; except for plants in the nutrition study, which received Hoagland solution on alternate days, as will be described later. All plants were grown in the greenhouse and watered daily. Natural light was supplemented with high-pressure sodium lamps to provide an average photosynthetic photon flux density of 400–500 $\mu E/m^2/s$ with a 16-h photoperiod. Greenhouse temperatures were 22–27/19–22°C day/night with a relative humidity of 30–70%.

The imazamethabenz was the commercial suspension concentrate formulation of imazamethabenz, containing 300 g a.i./L (Cyanamid Canada Inc., Markham, ON). The herbicide was applied to foliage of wild oat plants with an overhead trolley sprayer calibrated to deliver 100 L/ha at 210 kPa. Prior to spraying, the soil surface was covered with a layer of coarse vermiculite to prevent root absorption of the herbicide. The vermiculite was discarded 3 h after spraying. All plants were harvested 3 weeks after herbicide treatment for evaluation of imazamethabenz efficacy.

Influence of Nutrient Supply on Imazamethabenz Phytotoxicity

From the time of planting, 50 ml of Hoagland solution (Hoagland and Arnon, 1939) was applied to each pot every other day, with distilled water to field capacity on alternate days. There were four nutrient treatments: a) constant low nutrient with plants supplied with one-eighth-strength Hoagland solution throughout the experimental period (low); b) constant high nutrient with half-strength Hoagland solution supplied throughout (high); c) nutrient supply switching from one-eighth- to half-strength Hoagland solution immediately following herbicide application (low → high); and d) nutrient supply switching from half to one-eighth strength immediately after spraying imazamethabenz (high → low). Following emergence, the lengths of the first, second, and third leaves were measured in both nutrient treatments every second day until herbicide application. Just prior to spraying, the projected leaf area, viewed from above, and the total leaf area were measured with an image analyzer (Quantimet 970, Cambridge Instruments Ltd., Cambridge, UK); and the content of epicuticular wax of the second leaf was also determined (Oosterhuis et al. 1990). Imazamethabenz at doses of 200 and 400 g/ha was applied to plants at the three-leaf stage. At that time, the plants with high-nutrient treatment had two tillers, and most of the plants with low-nutrient supply had no tillers. There were eight replicates (each pot is one replicate in this and following experiments) in each treatment. The experiment was repeated once.

Influence of Tillering Capacity on Imazamethabenz Phytotoxicity

Among available pure lines of wild oat in our laboratory, CS 40 represented the line with the lowest tillering capacity and MON 73 represented the highest tillering line. Thus, in this experiment, both CS 40 and MON 73 were used to compare the sensitivity to imazamethabenz of pure lines with different tillering capacity. Imazamethabenz at 200 and 300 g/ha was applied to CS 40 and MON 73 plants at the two-leaf stage without tillers. There were six replicates in each treatment and the experiment was repeated once.

Influence of 2,4-D on Imazamethabenz Phytotoxicity

A foliar spray of imazamethabenz at 200 g/ha was applied to plants at the three-leaf stage without tillers. Four hours after spraying, a 10-µl drop of 2,4-D (Dow Elanco Canada Inc., Sarnia, ON) at a concentration of 6 µg/µl was applied with a micropipette to the furled fourth leaf of the main shoot apex. The 2,4-D application was repeated every second day for a total of five applications. There were seven replicates in each treatment, and the experiment was repeated twice.

Influence of GA_3 on Imazamethabenz Phytotoxicity

At the three-leaf stage, plants with one tiller were sprayed with imazamethabenz at 200 g/ha. Two days later a solution of 0.2% GA_3 (Fine Agrochemicals Ltd., Worcester, UK) containing 0.5% Agral 90 surfactant (ICI Chipman, Stoney Creek, ON) was sprayed on the seedlings using the same application method as for the herbicide. There were six replicates in each treatment and the experiment was repeated twice.

Experimental Design and Statistical Analysis

A completely randomized design was employed in each experiment. The analysis of variance (ANOVA) used was General Linear Model procedure of Statistical Analysis System (SAS Institute Inc., Cary, NC, USA). When applicable, a two-way ANOVA was used to detect the interaction between two factors. All raw data were subject to ANOVA analysis in all experiments except in the experiment of the effect of nutrient supply on the imazamethabenz phytotoxicity, where the raw data of the herbicide-treated plants in each nutrient supply treatment were transformed to the percentage of the corresponding nonherbicide-treated control before being subject to ANOVA analysis. In this nutrient experiment, only one set of experimental results was presented, but similar results were obtained from the repeated experiments. The treatment means in each experiment were separated by Fisher's Protected LSD test at the .05 level of significance.

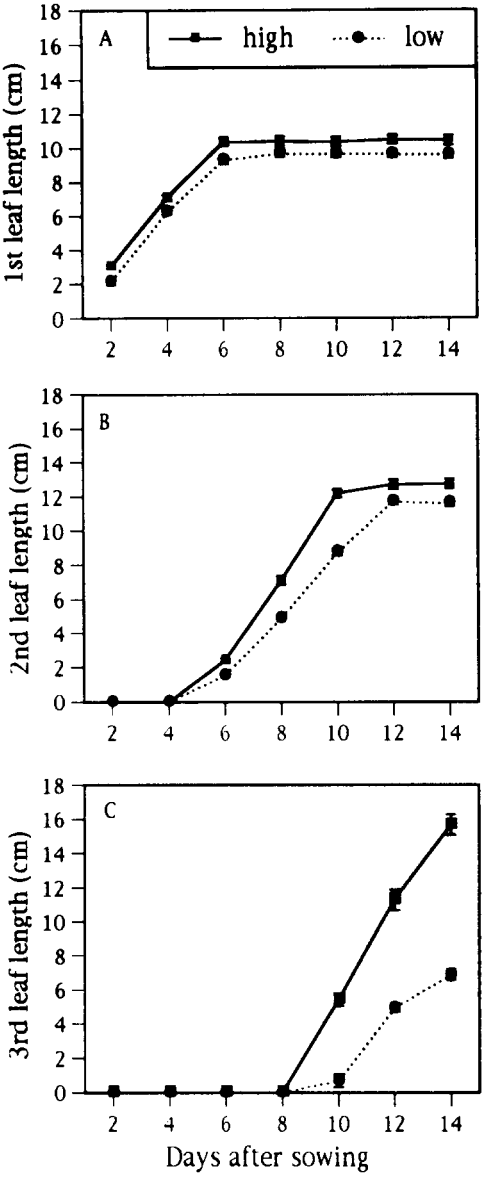

Fig. 1. Effect of nutrient levels on the growth of wild oat leaves. Plants under high-nutrient treatment were supplied with half-strength Hoagland solution. Plants under low-nutrient treatment were supplied with one-eighth-strength Hoagland solution. Vertical bars indicate standard errors.

Results

Influence of Nutrient Supply on Imazamethabenz Phytotoxicity

At the time of herbicide application, plants supplied with the higher level of nutrition had greater leaf length (Fig. 1) and larger total and projected leaf areas than those supplied with lower levels of nutrition (Table 1). Nutrient level had no significant effect on epicuticular wax content on the foliage (Table 1). In nonherbicide-treated plants, constant high-nutrient levels produced the most tillers, and constant low-nutrient levels resulted in the fewest tillers (Table 2).

Imazamethabenz induced more tillers in all nutrient treatments than in the nonherbicide-treated controls (Table 2). The lower herbicide dose (200 g/ha) tended to increase tiller fresh weight, whereas the higher dose (400 g/ha) reduced tiller fresh weight in all nutrient treatments except under constant low-nutrient regime. Imazamethabenz reduced main shoot growth under all nutrient regimes, with the least effect noted under constant low-nutrient supply. Better imazamethabenz phytotoxicity, as eval-

Table 1. Effect of nutrient supply on leaf area and epicuticular wax content in wild oat at the time of imazamethabenz application.

Nutrient supply	TLA (cm^2)	Projected leaf area		Wax on second leaf ($\mu g/cm^2$)
		cm^2	% of TLA	
High	15.5 ± 0.7[a]	4.0 ± 0.2	26 ± 1	11 ± 2
Low	11.5 ± 0.2	2.1 ± 0.1	18 ± 1	14 ± 2
F test	***	***	***	NS

TLA, total leaf area.
[a] Data are means ± SE.
*** Highly significant at $p < .001$; NS, not significant at $p > .05$.

Table 2. Effect of nutrient supply on the phytotoxicity of imazamethabenz in wild oat.[a]

Dose (g/ha)	Nutrient supply	% of respective control			
		Tiller number	Fresh weight		Dry weight of total shoot
			Main shoot	Total tillers	
0	high	(3.9)[b]	(4.7)	(3.8)	(1.4)
	low	(1.3)	(3.7)	(0.5)	(0.9)
	low → high	(2.9)	(4.4)	(2.4)	(1.3)
	high → low	(2.6)	(4.0)	(1.7)	(1.2)
200	high	244 ± 79[c]	52 ± 7	101 ± 9	64 ± 5
	low	253 ± 20	73 ± 4	219 ± 27	81 ± 2
	low → high	288 ± 14	45 ± 4	134 ± 18	56 ± 6
	high → low	228 ± 23	58 ± 7	137 ± 3	69 ± 6
400	high	274 ± 29	31 ± 4	33 ± 9	35 ± 6
	low	407 ± 34	47 ± 2	318 ± 24	65 ± 1
	low → high	271 ± 31	19 ± 2	30 ± 5	24 ± 2
	high → low	261 ± 15	37 ± 4	93 ± 19	51 ± 7
LSD (0.05)		81	14	48	15

[a] A 2 × 4 factorial ANOVA was analyzed on data of transformed percentage of control for herbicide-treated plants. Within nutrient-supply treatments, there was a significant effect of imazamethabenz at $p < .01$ on all evaluated parameters except on tiller number at $p < .05$. Within imazamethabenz treatments, there was a significant effect on nutrient supply at $p < .01$ on all parameters except on tiller number at $p < .05$. The interaction of imazamethabenz dose × nutrient supply was significant at $p < .01$ in total tiller fresh weight and at $p < .05$ in tiller number.
[b] Data in parentheses are actual values with fresh and dry weights in grams per plant.
[c] Data are means ± SE.

uated by total shoot biomass, was obtained in wild oat, switched from low- to high-nutrient supply rather than the reverse sequence. Specifically, the herbicide activity, from best to worst, varied with nutrient treatments as follows: low → high ≈ constant high > high → low > constant low (Table 2).

Influence of Tillering Capacity on Imazamethabenz Phytotoxicity

Wild oat pure-line CS 40 was taller and had fewer tillers than MON 73 in nonherbicide-treated plants (Table 3). At both doses of imazamethabenz (200 and 300 g/ha), tillering was increased in CS 40, whereas the tillering response of MON 73 to the herbicide was dose dependent, with low dose increasing, and high dose reducing, tiller number. Tiller fresh weight of CS 40 was increased following all applications of imazamethabenz, but was decreased in MON 73 by both doses. Imazamethabenz inhibited the growth of the main shoot in both wild oat lines, but the herbicide reduced total shoot biomass more in MON 73 than in CS 40 (Table 3).

Influence of 2,4-D and GA_3 on Imazamethabenz Phytotoxicity

In nonherbicide-treated plants, neither 2,4-D (Table 4) nor GA_3 (Table 5) had any significant effect on wild oat tillering. When wild oat plants were treated with imazamethabenz at 200 g/ha, both 2,4-D and GA_3 reduced herbicide-induced tillering, especially

Table 3. Responses of wild oat pure lines CS 40 and MON 73 to imazamethabenz.[a]

Pure line	Dose (g/ha)	Main shoot height (cm)	Tiller number	Fresh weight (g) Main shoot	Fresh weight (g) Total tillers	Dry weight of total shoot (g)
CS 40	0	38 ± 0.9[b]	0.8 ± 0.2	2.0 ± 0.1	0.2 ± 0.1	0.4 ± 0.03
	200	28 ± 0.8	4.8 ± 0.4	0.9 ± 0.1	0.6 ± 0.1	0.3 ± 0.02
	300	28 ± 0.7	5.0 ± 0.3	0.7 ± 0.05	0.4 ± 0.06	0.2 ± 0.02
MON 73	0	30 ± 0.9	2.7 ± 0.4	1.1 ± 0.1	0.6 ± 0.1	0.3 ± 0.03
	200	25 ± 0.6	4.9 ± 0.8	0.4 ± 0.01	0.2 ± 0.04	0.1 ± 0.01
	300	23 ± 0.5	1.7 ± 0.6	0.3 ± 0.02	0.1 ± 0.03	0.1 ± 0.01
LSD (0.05)		2	1.3	0.2	0.2	0.06

[a] A 2 × 3 factorial ANOVA was analyzed. Within pure-line treatments, there was a significant effect of imazamethabenz at $p < .01$ in all evaluated parameters. Within imazamethabenz treatments, there was a significant effect of pure line at $p < .01$ in all parameters except in tiller number and total tiller fresh weight at $p < .05$. The interaction of pure line × imazamethabenz was significant at $p < .01$ in tiller number and fresh weights of the main shoot and total tillers, and was significnt at $p < .05$ in the main shoot height.
[b] Data are mean ± SE.

Table 4. Effect of 2,4-D (−, without; +, with) on the phytotoxicity of imazamethabenz in wild oat.[a]

Dose (g/ha)	2,4-D	Tiller number	Fresh weight (g) Main shoot	Fresh weight (g) Total tillers	Dry weight of total shoot (g)
0	−	3.3 ± 0.3[b]	5.0 ± 0.4	3.0 ± 0.5	1.7 ± 0.2
	+	4.1 ± 0.3	4.0 ± 0.2	3.9 ± 0.6	1.6 ± 0.1
200	−	8.3 ± 1.2	1.6 ± 0.1	2.3 ± 0.3	0.7 ± 0.1
	+	5.7 ± 0.7	1.6 ± 0.2	2.2 ± 0.4	0.7 ± 0.1
LSD (0.05)		2.0	0.5	1.1	0.3

[a] A 2 × 2 factorial ANOVA was analyzed. Within 2,4-D treatments, there was a significant effect of imazamethabenz at $p < .01$ in all evaluated parameters. Within the imazamethabenz treatments, there was a significnt effect of 2,4-D at $p < .05$ in tiller number and the main shoot fresh weight. There was no interaction of 2,4-D × imazamethabenz.
[b] Data are mean ± SE.

GA_3. However, 2,4-D had no significant effect on the fresh weights of main shoot and total tillers, or on the dry weight of the total shoot in herbicide-treated plants (Table 4). GA_3 increased the height of main shoots only in the plants not treated with imazamethabenz (Table 5). Following imazamethabenz application, GA_3 treatment enhanced herbicide phytotoxicity, with further reduction in the fresh weights of main shoot and total tillers and total shoot biomass, although GA_3 alone had little effect on those parameters.

Discussion

This study demonstrated that imazamethabenz controlled wild oat more effectively when plants were grown with high-nutrient supply (Table 2). A similar enhancement in herbicide phytotoxicity has been reported with diclofop and fluazifop ((±)-2-[4-[[5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid) in oat (Andrews et al. 1989, Dickson et al. 1990), with glyphosate (*N*-(phosphonomethyl)-glycine) in quackgrass (McIntyre and Hsiao 1982), and with picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) in leafy spurge (Regimbal and Martin 1985).

Nutrition level had little effect on epicuticular wax content of wild oat foliage (Table 1), and consequently nutrient treatments should not greatly affect imazamethabenz absorption. Work by Dickson et al. (1990) supports such an assertion. They found that the uptake of [^{14}C]-fluazifop in oat was not significantly changed under different levels of nitrogen supply. Increasing the projected leaf area of plants at high-nutrient levels (Table 1) should result in greater herbicide interception, which in turn may enhance herbicide phytotoxicity (Lutman and Sagar 1975). Such an effect can only partially account for better imazamethabenz efficacy with the high-nutrient treatment, because imazamethabenz was much less effective in wild oat when the nutrient supply was decreased after herbicide application (Table 2).

Table 5. Effect of GA_3 (−, without; +, with) on the phytotoxicity of imazamethabenz in wild oat.[a]

Dose (g/ha)	GA_3	Main shoot height (cm)	Tiller number	Fresh weight (g) Main shoot	Fresh weight (g) Total tillers	Dry weight total shoot (g)
0	−	54 ± 1[b]	2.3 ± 0.1	13.0 ± 0.5	5.2 ± 0.5	3.8 ± 0.3
	+	71 ± 3	2.5 ± 0.3	14.4 ± 0.1	6.5 ± 0.7	3.7 ± 0.2
200	−	30 ± 2	8.2 ± 0.5	4.4 ± 0.2	4.9 ± 0.8	1.7 ± 0.1
	+	30 ± 1	1.9 ± 0.6	2.5 ± 0.3	0.8 ± 0.3	0.9 ± 0.1
LSD (0.05)		4	1.2	0.8	1.5	0.5

[a] A 2 × 2 factorial ANOVA was analyzed. Within GA_3 treatments, there was a significant effect of imazamethabenz at $p < .01$ in all evaluated parameters. Within the imazamethabenz treatments, there was a significant effect of GA_3 at $p < .01$ in the main shoot height, tiller number, and total shoot dry weight and at $p < .05$ in total tiller fresh weight but not significant in the main shoot fresh weight. The interaction of GA_3 × imazamethabenz was significant at $p < .01$ in all parameters.
[b] Data are mean ± SE.

In foliar application imazamethabenz enters the phloem and moves with the photosynthate flow (Little and Shaner 1991). Increased nutrient supply can increase photosynthesis and thereby photosynthate transport (Kupka 1992). At high nitrogen levels, enhanced fluazifop phytotoxicity in oat was related to increased transport of herbicide to apical meristems (Dickson et al. 1990). In the present study, increased activity of imazamethabenz in the main shoot of wild oat in the high-nutrient treatment (Table 2) was probably caused by a similar mechanism as was found with fluazifop. Increased nutrient availability reduced apical dominance and increased growth activity of inhibited tiller buds (McIntyre 1990). This may explain the increased susceptibility of wild oat tillers to imazamethabenz in plants with a high-nutrient supply (Table 2).

The present study indicated that the influence of high-nutrient supply on imazamethabenz phytotoxicity was time dependent with the nutrient condition of plants after spraying being more critical in determining herbicide activity than the nutrient status before spraying (Table 2). A similar result was also shown for diclofop (Andrews et al. 1989). The increase in photosynthesis accompanying the switch from low to high nutrient supply at time of herbicide spraying should increase the transport of photosynthate and herbicide out of the treated leaf, which may be associated with increased imazamethabenz activity on such plants and decreased activity in plants switched from high to low nutrient supply at the time of herbicide application.

Somody et al. (1984) observed a relationship between herbicide tolerance and limited tillering in wild oat. The reduced imazamethabenz efficacy in CS 40 plants, a limited tillering line of wild oat, and better herbicide efficacy in MON 73, a strongly tillering line (Table 3), support this observation. Our results strongly support our hypothesis that imazamethabenz is more effective in wild oat lines with lower apical dominance than in the lines with higher apical dominance.

Imazamethabenz-induced tillering in wild oat was reduced by 2,4-D (Table 4) and more so by GA_3 (Table 5). This effect was due at least partially to the ability of these two growth regulators to maintain apical dominance (Rood 1985, Sharif and Dale 1980). But these two growth regulators affected the overall phytotoxicity of imazamethabenz in different ways, with 2,4-D having little effect (Table 4) and GA_3 increasing imazamethabenz phytotoxicity (Table 5). Applied GA_3 increased the height of non-herbicide-treated wild oat plants (Table 5), which was consistent with the results in many other plant species (Macháčková 1992). Such growth enhancement due to GA_3 application may increase imazamethabenz translocation to those GA_3-stimulated-growth regions, thus improving herbicide activity. The ability of GA_3 to inhibit tillering enhances the effectiveness of imazamethabenz in this regard.

The increased phytotoxicity of imazamethabenz found in tillers of wild oat with a high-nutrient supply and in tillers of MON 73 supports our hypothesis that lowering apical dominance increases imazamethabenz activity in tillers. The reduced number of tillers caused by the application of 2,4-D and GA_3 further supports our previous hypothesis (Chao et al. 1993) that increased tillering following sublethal doses of imazamethabenz treatment is the result of the release of apical dominance.

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References

Andrews M, Dickson RL, Foreman MH, Dastgheib F, Field RJ (1989) The effect of different external nitrate concentrations on growth of *Avena sativa* cv. Amuri treated with diclofop-methyl. Ann Appl Biol 114:339–348

Brown BT, Foster C, Phillips JN, Rattigan BM (1979) The indirect role of 2,4-D in the maintenance of apical dominance in decapitated sunflower seedlings (*Helianthus annuus* L.). Planta 146:475–480

Chao JF (1993) Interactions between tillering and phytotoxicity of imazamethabenz in wild oat (*Avena fatua* L.). M.Sc. Thesis, University of Regina, Regina, SK, Canada

Chao JF, Hsiao AI, Quick WA (1993) Effect of imazamethabenz on the main shoot growth and tillering of wild oat (*Avena fatua* L.). J Plant Growth Regul 12:141–147

Chao JF, Hsiao AI, Quick WA, Hume JA (1994) Effect of decapitation on absorption, translocation, and phytotoxicity of imazamethabenz in wild oat (*Avena fatua* L.). J Plant Growth Regul 13:153–158

Dickson RL, Andrews M, Field RJ, Dickson EL (1990) Effect of water stress, nitrogen, and gibberellic acid on fluazifop and glyphosate activity on oats (*Avena sativa*). Weed Sci 38:54–61

Evans LT, Wardlaw IF, William CN (1964) Environmental control of growth. In: Barnard C (ed) Grasses and grasslands. Macmillan, London, pp 102–125

Fletcher GM, Dale JE (1974) Growth of tiller buds in barley: Effects of shade treatment and mineral nutrition. Ann Bot 38:63–76

Hoagland DR, Arnon DI (1939) The water culture method of growing plants without soil. Circ Calif Agric Exp Stn No 347

Johnson BJ, Murphy TR (1991) Sequential herbicide and plant growth regulator treatments on bermudagrass (*Cynodon* spp.). Weed Technol 5:607–611

Kupka J (1992) Physiology of mineral nutrition of plants. In: Šebánek J (ed) Plant physiology. Elsevier, Amsterdam, pp 159–198

Leopold AC (1949) The control of tillering in grasses by auxin. Am J Bot 36:437–440

Little DL, Shaner DL (1991) Absorption and translocation of the imidazolinone herbicides. In: Shaner DL, O'Connor SL (eds) The imidazolinone herbicides. CRC Press, Boca Raton, pp 53–70

Lutman PJW, Sagar GR (1975) The influence of the nitrogen status of oat plants (*Avena sativa* L.) on the interception and retention of foliar spray. Weed Res 15:217–220

Macháčková I (1992) Growth and growth regulators. In: Šebánek J (ed) Plant physiology. Elsevier, Amsterdam, pp 215–271

McIntyre GI (1990) The correlative inhibition of bud growth in perennial weeds: A nutritional perspective. Rev Weed Sci 5:27–48

McIntyre GI, Hsiao AI (1982) Influence of nitrogen and humidity on rhizome bud growth and glyphosate translocation in quackgrass (*Agropyron repens*). Weed Sci 30:655–660

Nalewaja JD, Woznica Z (1985) Environment and chlorsulfuron phytotoxicity. Weed Sci 33:395–399

Naylor JM, Jana S (1976) Genetic adaptation for seed dormancy in *Avena fatua*. Can J Bot 54:306–312

Oosterhuis DM, Wullschleger SD, Hampton RE, Ball RA (1990) Physiological response of rice (*Oryza sativa*) to fenoxaprop. Weed Sci 38:459–462

Regimbal GA, Martin AR (1985) The influence of growth regulators and nitrogen on leafy spurge (*Euphorbia esula*) control with picloram. Weed Sci 33:109–113

Rood SB (1985) Application of gibberellic acid to control tillering in early-maturing maize. Can J Plant Sci 65:901–911

Shaner DL, Umeda K, Ciarlante DR, Los M (1982) AC 222,293 a new postemergent herbicide for cereals: Greenhouse studies. Proc Brit Crop Prot Conf Weeds, pp 25–38

Sharif R, Dale JE (1980) Growth-regulating substances and the growth of tiller buds in barley; effect of IAA and GA_3. J Exp Bot 31:1191–1197

Smith AM, Chow PNP (1990) The influence of Agral 90 surfactant on the activity of imazamethabenz in wild oats (*Avena fatua* L.). Weed Res 30:355–362

Somody CN, Nalewaja JD, Miller SD (1984) Wild oat (*Avena fatua*) and *Avena sterilis* morphological characteristics and response to herbicides. Weed Sci 32:353–359

Woodward EJ, Marshall C (1988) Effects of plant growth regulators and nutrient supply on tiller bud outgrowth in barley (*Hordeum elistichum* L.). Ann Bot 61:347–354