J Plant Growth Regul (1997) 16:173–179

Journal of Plant Growth Regulation

Tillers Do Not Influence Phytotoxicity of Imazamethabenz in Wild Oat (*Avena fatua*)

J. F. Chao,[1] A. I. Hsiao,[2,*] and W. A. Quick[1]

[1]Department of Biology, University of Regina, Regina, SK S4S 0A2, and [2]Agriculture and Agri-Food Canada, Research Station, Box 440, Regina, SK S4P 3A2, Canada

Received June 4, 1997; accepted June 5, 1997

Abstract. The response of wild oat to imazamethabenz varies with the growth stage, but the role of tillers in this regard is unclear. Removal of tillers at the three-leaf stage before spraying with imazamethabenz did not significantly affect the total shoot fresh weight measured 3 weeks later. The leaf area and dry weight of intact plants at the three-leaf stage were 17–21% greater than for plants with coleoptilar and first leaf main shoot tillers (T0 and T1) removed. The greater leaf area may have increased herbicide interception per plant. Similar fresh weight reductions in main shoot, total tillers, and total shoots were found whether imazamethabenz was applied to the plant at the two-leaf without tillers or the three-leaf with two tillers stage. Imazamethabenz applied only to the main shoot reduced total shoot dry weight more than an equivalent amount of imazamethabenz applied only to tiller T1 or applied over the whole shoot. Imazamethabenz had the least inhibitory effect on whole plant growth when applied only to T1. When ^{14}C-herbicide was applied to the first main shoot leaf of plants at the three-leaf stage with two tillers, the ^{14}C translocated 38% to roots, 33% to the main shoot, and nearly 30% to all tillers. When ^{14}C-herbicide was applied to the first leaf of T1 then the ^{14}C translocated 50% to T1, 25% to the main shoot, 20% to roots, and 5% to all other tillers. The translocation pattern and fresh weight values suggested that the presence of early tillers during herbicide application neither increased nor decreased imazamethabenz efficacy in wild oat.

Key Words. Tillering—Translocation—Phytotoxicity—Tiller removal

Abbreviation: PPFD, photosynthetic photon flux density.
*Author for correspondence.

Wild oat is a troublesome annual grass weed that begins to produce tillers around the three-leaf stage, a process that aids the plant in establishing itself and increases its adaptive ability. In this paper *tiller* refers to any lateral shoot that is externally visible above the subtending leaf sheath, and tiller designation follows the same system as described previously (Chao et al. 1993, 1994b).

Application of sublethal doses of methyl ester of imazamethabenz-methyl, (±)-2-[4,5-dihydro-4-methyl-4-(methylethyl)-5-oxo-1*H*-imidazol-2-yl]-4(and 5)-methylbenzoic acid (3:2), applied to wild oat at Zadoks' stage 12,20 (Zadoks et al. 1974) stopped main shoot growth but increased tillering (Chao et al. 1993). Smith and Chow (1990) suggested that the reduced effectiveness of low doses of imazamethabenz at this stage was because of the lack of exposure of the tillers to the herbicide. They reported that wrapping visible tillers to avoid their exposure to spraying solution decreased imazamethabenz phytotoxicity in both tillers and in the main shoot of wild oat (Smith and Chow 1990). The increased main shoot control when tillers were exposed to the spraying solution was interpreted as caused by translocation of imazamethabenz from the tillers to the main shoot. The greater reduction in tillers fresh weight when tillers were exposed to the herbicide led the authors to emphasize the importance for effective control of contact between the herbicide solution and the preexisting tillers. Any increase in the number of emerged tillers would provide more leaf surface for interception of foliar applied herbicides (McIntyre 1990 and references therein) and logically should increase herbicide phytotoxicity. However, the effectiveness of imazamethabenz control on wild oat was reported to decrease as plants developed tillers (Smith and Chao 1990). The decreased control by imazamethabenz on field-grown wild oat at later stages was interpreted as being caused by the presence of tillers during spraying (Harker and O'Sullivan 1991, Morrison and Mayert 1982, van Hoogstraten

1983). Thus, the effect of early tillers on the performance of imazamethabenz applied to wild oat has remained controversial. The objectives of this study were: (1) to clarify whether early tillers present at the time of application increase or decrease imazamethabenz efficacy on wild oat; (2) to determine whether the placement of imazamethabenz on different parts of the plant had any effect on its phytotoxicity; and (3) to determine the absorption and translocation pattern of [^{14}C]imazamethabenz applied to tillers and to the main shoot.

Materials and Methods

Plant Materials

A genetically uniform line of *Avena fatua* L., CS 40, was used in all experiments. Seeds were germinated for 4 days at room temperature on moist filter paper. For the efficacy study, five germinated seeds were planted 2 cm deep in each 12.5-cm-diameter pot containing sandy loam soil. When plants reached the one-leaf stage, they were thinned to three/pot and fertilized at that time with 50 mL of 20:20:20 N:P:K/pot at 3 g/liter. Plants to be used to assess how tillers present at the time of herbicide application affected the efficacy of imazamethabenz were maintained in the greenhouse. Plants were watered daily on the soil surface. Natural light was supplemented with high pressure sodium lamps, with a 16-h photoperiod at an average photosynthetic photon flux density (PPFD) of 400–500 μE $m^{-2}s^{-1}$. Greenhouse temperatures ranged from 22 to 27/19 to 22°C day/night with a relative humidity of 30–70%.

For the herbicide placement study, plants were grown under the same conditions as in the efficacy study above except that they were maintained in a growth chamber at 20 ± 1/15 ± 1°C day/night, 50% relative humidity under a photoperiod approximately 300 μE $m^{-2}s^{-1}$ PPFD.

For the radioisotope study, silica sand-filled styrofoam cups (6.7-cm diameter, 8.0-cm depth, fitted with drainage holes) were used, each containing three wild oat seeds planted at a depth of 2 cm. The sand was moistened thoroughly with distilled water and then saturated with approximately 30 mL of 1/4 strength standard Hoagland's solution (Hoagland and Arnon 1939). Plants were placed in the growth chamber at 20 ± 1/15 ± 1°C day/night, 50% relative humidity under a 16-h photoperiod of approximately 425 μE $m^{-2}s^{-1}$ PPFD. On emergence the seedlings were watered daily with 1/4 strength Hoagland's solution. Plants were thinned to one/pot at the one-leaf stage.

Effect of Tillers Present at the Time of Application on Imazamethabenz Efficacy

The commercial suspension concentrate formulation of imazamethabenz, Assert 300 SC, was used in all experiments. It contained 300 g a.i./liter. Imazamethabenz at 300 g a.i./liter was applied to the foliage of plants at 300 g/ha with a moving nozzle cabinet-type sprayer calibrated to deliver 100 liters/ha at 210 Kpa. Before spraying, the soil surface was covered with a layer of coarse vermiculite to prevent root absorption of the herbicide. The vermiculite was removed 3 h after spraying.

There were two experiments in this study, in both experiments a completely randomized design with five replicates/treatment was used, and each experiment was repeated once. Before herbicide application at growth stage 13,22 (three-leaf stage with two tillers) in experiment 1, the projected leaf area (top view) of both the main shoot and the T0 and T1 tillers present were determined. Values were determined with an image analyzer (Quantimet 970, Cambridge Instruments Ltd., Cambridge, UK CB3 8EL) using plants from seven pots of a companion set of wild oat plants. The dry weight of each plant from this companion set was also determined. In experiment 1, imazamethabenz was applied to plants at growth stage 13,22. Just before herbicide application, the tillers present in plants of half of the ten pots were removed. T0 (the coleoptilar tiller) was cut at the soil surface, and T1 (the first leaf tiller of the main shoot) was cut at the top of the leaf sheath. Tillers were retained on the plants in the remaining five pots for exposure to spray solution during herbicide application. Plants were harvested 3 weeks after herbicide treatment.

Table 1. Effect on the efficacy of imazamethabenz of tillers present at the time of herbicide application on wild oat plants at stage 13,22.

Dose (g ha^{-1})	Tillers present or not	Main shoot FW[a] (g)	Total tillers FW (g)	Total shoots FW (g)	Total tiller number
0	Yes	3.65 ± 0.31[b]	1.25 ± 0.24	4.90 ± 0.54	9.0 ± 1.8
	No	3.15 ± 0.19	0.63 ± 0.09	3.78 ± 0.27	7.0 ± 0.9
300	Yes	1.06 ± 0.08	0.89 ± 0.14	1.95 ± 0.22	20.4 ± 1.3
	No	1.28 ± 0.09	1.03 ± 0.21	2.31 ± 0.29	23.4 ± 3.0

[a] FW, fresh weight at termination of experiment.
[b] Data are means per plant with standard errors.

In experiment 2, imazamethabenz was sprayed on plants at two different growth stages, 12,20 (two-leaf stage without tiller) and 13,22, with the same application conditions. Under our growth conditions a 4-day interval separated growth stage 12,20 and 13,22. All plants were harvested at the same day, 25 days after herbicide application to plants at stage 12,20 and 21 days after application at stage 13,22. Thus, at harvest the plants in both treated stages were of the same chronological age.

Study of Absorption and Translocation of [^{14}C]Imazamethabenz

[^{14}C]Imazamethabenz (labeled in the 4 position of the imidazolin ring, specific activity of 39.55 μCi/mg) with a radiochemical purity of >98% was obtained from American Cyanamid Co. The preparation and application of the labeled imazamethabenz were as described previously (Chao et al. 1994b). Solid [^{14}C]imazamethabenz was dissolved in 10 mL of methanol as a stock solution containing 8.7 μCi/mL and 220 μg of imazamethabenz/mL. The required volume containing 5.625 μCi was taken from the stock solution, evaporated to dryness, and redissolved into 0.5 mL of 3,000 ppm commercial suspension concentrate formulated imazamethabenz (300 g a.i./liter or 10 mM) solution diluted with distilled water. Two 2-μL droplets were applied by micropipettes to the adaxial midsection of the first leaf lamina of the main shoot or T1 (one 2-μL droplet each side of the middle vein). After treatment of the plants, the sand was kept moist but not leached.

Plants were harvested 24, 48, and 96 h after treatment and divided into five parts: treated leaf, T1 tiller, main shoot, all other tillers, and roots. The surface residues were washed off with three rinses of 10 mL of 0.1% (v/v) Tween 20 solution (polyoxyethylene (20) sorbitan monolaurate) over the treated area. The ^{14}C in each rinse was assayed by liquid scintillation. Separate analyses of standards revealed that this procedure removed essentially all unabsorbed ^{14}C. The sum of radioactivity from these washes was considered to constitute unabsorbed herbicide. Each plant part was cut into strips and combusted in a biological sample oxidizer (model OX 500, R. J. Harvey Instrument

Table 2. Effect on the efficacy of imazamethabenz of tillers present at the time of herbicide application on wild oat plants.[a]

Dose ($g\ ha^{-1}$)	Tillers present or not	Main shoot FW[b] (g)	Total tillers FW (g)	Total shoots FW (g)	Total tiller number
0	Yes	2.43 ± 0.28[c]	1.67 ± 0.18	4.10 ± 0.54	9.0 ± 1.8
	No	2.41 ± 0.02	1.25 ± 0.19	3.97 ± 0.11	7.0 ± 0.9
300	Yes	1.06 ± 0.08	0.89 ± 0.14	1.95 ± 0.21	20.3 ± 1.3
	No	0.92 ± 0.11	1.27 ± 0.23	2.19 ± 0.34	21.4 ± 1.4

[a] Experiment 2 with tillers present at stage 13,22 or with tillers absent at stage 12,20 at time of herbicide application.
[b] FW, fresh weight at termination of experiment.
[c] Data are means per plant with standard errors.

Corp.) The roots were washed under a stream of water to remove sand and then dried at room temperature before oxidation. The trapped $^{14}CO_2$ was quantified by liquid scintillation. The overall recovery of ^{14}C in the experiment was 90 ± 4%.

A completely randomized design with five replicates/treatment was used at each harvest time. The experiment was repeated once. All data in each experiment were subjected to analysis of variance. Treatment means were separated by Fisher's protected least squares difference test at $p = 0.05$.

Table 3. Projected leaf area and dry weight of the wild oat plant at growth stage 13,22 determined before imazamethabenz application.

	Projected leaf area (cm^2)	Dry weight (mg)
Main shoot	14.19 ± 0.70[a]	130.9 ± 5.0
Tillers	3.05 ± 0.21	35.1 ± 2.7
Whole plant	17.24 ± 0.80	166.0 ± 7.3

[a] Data are means per plant with standard errors.

Results and Discussion

Effect of Tillers Present at the Time of Application on the Efficacy of Imazamethabenz

Tillers present at the time of herbicide application did not affect imazamethabenz activity in wild oat (Tables 1 and 2). When tillers were retained on the plant and exposed to the spray solution, the activity of imazamethabenz was the same as when tillers were removed (Table 1). There were no differences in fresh weight of the main shoot and total shoots or in the number of total tillers in herbicide-treated plants, whether tillers had been removed or not.

Existing tillers treated at stage 13,22 accounted for 17.25% of the projected leaf area (Table 3). We have found the projected leaf area to be proportional to the herbicide interception (Xie et al. 1995). However, the presence of tillers also increased plant biomass and contributed 20.6% to the shoot dry weight. Therefore the increased amount of herbicide intercepted by plants with exposed tillers, if presented as herbicide/unit of biomass, may not differ significantly from the value for plants lacking tillers or with tillers removed at time of spraying. This interpretation may also apply to the results of experiment 2, in which imazamethabenz was sprayed on plants at stages 12,20 and 13,22 (Table 2). In experiment 2 there was no significant difference in the fresh weight of the main shoot, total tillers, and total shoots whether tillers were or were not present at the time of spraying.

The data from both experiments 1 and 2 conflict with the report by Smith and Chow (1990) in which tiller exposure to spray solution reduced main shoot fresh weight and increased imazamethabenz phytotoxicity. In their report, the control effect was compared between plants exposed to applied herbicide and plants with tillers wrapped to avoid herbicide deposition. Thus, the apparent increased overall phytotoxicity of imazamethabenz by accompanying tiller exposure to spray solution was probably the result of increased interception of herbicide. This interpretation is supported by the data in Table 3 of this paper.

The maximum tillering capacity of a given species is determined by the plant inheritance per se. Tillering is a very plastic feature, greatly influenced by external factors such as light, nutrition, and soil compaction (Carlsson and Callaghan 1990, Casal et al. 1986, Deregibus et al. 1985, Hucl and Baker 1990, Jewiss 1972). As with other annual grasses (Takahashi 1991), wild oat tiller initiation and development occur only at a certain stage of growth (tillering stage) and do not necessarily increase with the advancement of growth stages. Wild oat plants grown in high nutrient level produce more and better established tillers than plants grown in low nutrient media but are better controlled by imazamethabenz (Chao et al. 1994a). This suggests that the presence of tillers at the time of application does not necessarily decrease the efficacy of imazamethabenz. The superior control in the field, when imazamethabenz is applied to one- to three-leaf stage, compared with the three- to four-leaf stage, may be caused mainly by more effective competition from the crop plants at the later stage.

Table 4. Effect on the phytotoxicity of imazamethabenz of its placement on different parts of the plant at stage 14,21.

Placement of imazamethabenz on plant parts	Main shoot FW[a] (g)	Tiller T1 FW (g)	Tiller T2 FW (g)	Tiller T3 FW (g)	Total tiller FW (g)	Total shoot DW[b] (g)	Total tiller number
Control	2.89 ± 0.12[c]	1.57 ± 0.14	1.24 ± 0.01	0.73 ± 0.10	4.14 ± 0.17	1.56 ± 0.07	2.0 ± 0.2
Main shoot only	1.02 ± 0.16	0.69 ± 0.16	0.26 ± 0.07	0.17 ± 0.04	2.02 ± 0.19	0.64 ± 0.09	3.0 ± 0.1
Tiller T1 only	2.32 ± 0.25	0.17 ± 0.03	1.07 ± 0.12	0.76 ± 0.09	3.20 ± 0.33	1.18 ± 0.13	2.6 ± 0.1
Whole shoots	1.77 ± 0.15	0.26 ± 0.03	0.68 ± 0.12	0.45 ± 0.13	1.90 ± 0.27	0.78 ± 0.08	2.7 ± 0.3

[a] FW, fresh weight at termination of experiment.
[b] DW, dry weight.
[c] Data are means per plant with standard errors.

Argument persists as to whether tillering is a wasteful overgrowth or has an active role in contribution to crop productivity (Jewiss 1972, Simmons and Lauer 1986 and references therein). Interestingly, in the non–herbicide-treated control treatment, the main shoot fresh weight increased in plants where tillers were retained compared with main shoot fresh weight of plants with tillers removed (Tables 1 and 2). This implies that such early developed tillers as coleoptilar and first leaf tillers do make a contribution to the main shoot growth.

Effect on Phytotoxicity of the Placement of Imazamethabenz on Different Plant Parts

In the previous two experiments, although equivalent amounts of herbicide were applied to each plant, the total amount of herbicide actually intercepted per plant with tillers present was different from that of the plants without tillers or with tillers removed. Our previous studies (Xie et al. 1996) on absorption, translocation, and phytotoxicity of labeled imazamethabenz had relied on droplets applied to the adaxial section of the second lamina of the main shoot. In this experiment, an equivalent amount of imazamethabenz was applied to each plant but with different placements. When imazamethabenz was applied to the whole plant, both on the main shoot and the preexisting tillers, the efficacy was less than when an equivalent amount of imazamethabenz was applied to the main shoot only (Table 4). The differences in tiller number under growth chamber conditions (Table 4) and earlier experiments (Tables 1 and 2) are caused mainly by the higher temperatures and light intensities under summer greenhouse conditions. The reductions in dry weight of total shoots and in the fresh weight of the main shoot and tillers (excluding T1) were least when imazamethabenz was applied to T1 only. This implied that the most active imazamethabenz action and the most useful site for efficient control of wild oat were at the main shoot. This experiment demonstrated the importance of direct contact between preexisting tillers and herbicide solution for effective control on these tillers. Herbicide efficacy on the preexisting tiller T1 was improved by directly delivering imazamethabenz solution with a micropipette to the T1 only or to both the main shoot and T1. Since the fresh weight of the main shoot was reduced in plants

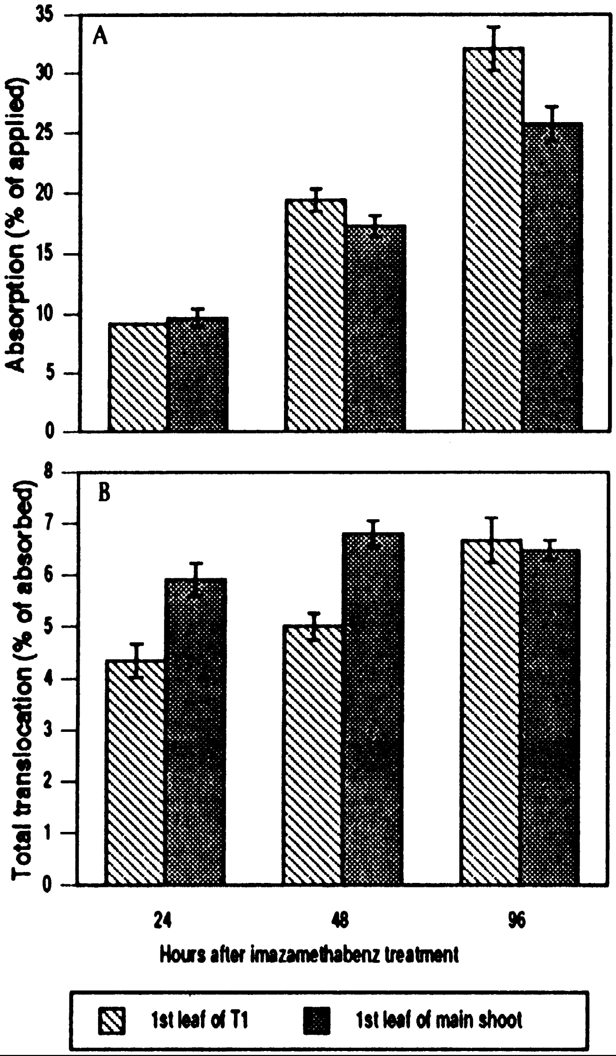

Fig. 1. Absorption (A) and total translocation (B) of [^{14}C]imazamethabenz when applied to first leaf of T1 or first leaf of main shoot of wild oat plant at stage 13,22. *Vertical bars* indicate standard errors.

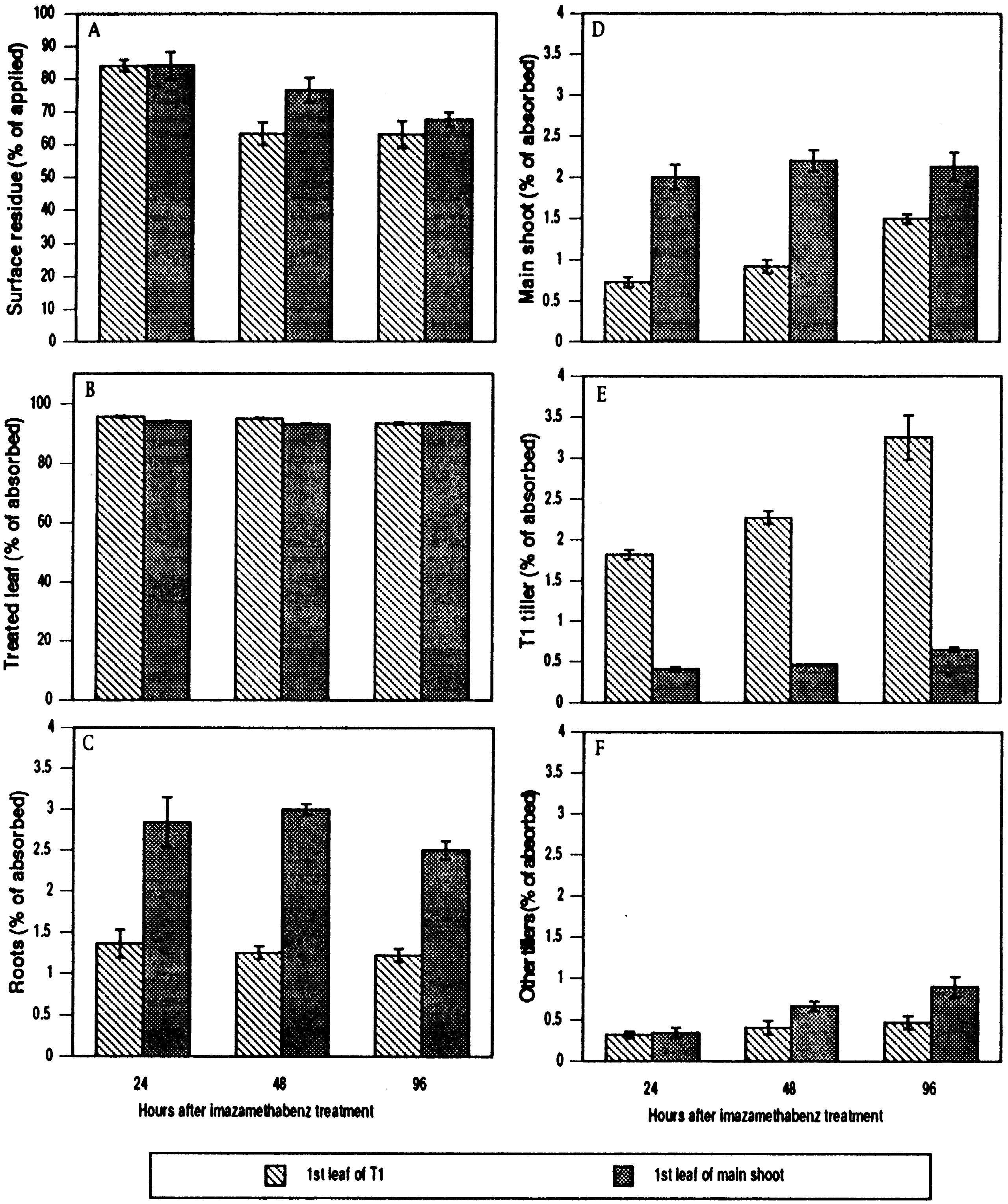

Fig. 2. Distribution of [^{14}C]imazamethabenz in the whole wild oat plant (A–F) when applied to first leaf of T1 or first leaf of main shoot at stage 13,22. *Vertical bars* indicate standard errors.

treated with imazamethabenz on T1 only, and since application of imazamethabenz to the main shoot only resulted in the reduction of the fresh weight of the preexisting tiller T1, we inferred that there was imazamethabenz translocation between tillers and the main shoot. The results of the study with labeled imazamethabenz confirmed this inference.

Study of Absorption and Translocation of [^{14}C]-Imazamethabenz

[^{14}C]Imazamethabenz absorption and total translocation are shown in Fig. 1. Increased herbicide absorption by the first lamina of T1 was probably because the first lamina of T1 was younger and therefore may have had less wax and a thinner cuticle layer than the first lamina of the main shoot. The distribution of [^{14}C]imazamethabenz in different parts of the plant is displayed in Fig. 2. Only 7% of absorbed imazamethabenz was translocated with 93% of absorbed herbicide remaining in treated leaves (Fig. 2B). This is consistent with our previous report (Chao et al. 1994b). Of the translocated imazamethabenz in T1 treatment, 50% remained in T1 (excluding the treated first leaf of T1), 25% and 20% were, respectively, allocated to the main shoot and roots, and 5% was detected in other tillers. However, in the treatment in which [^{14}C]imazamethabenz was applied to the first lamina of the main shoot, the allocation of total translocated imazamethabenz 96 h after herbicide application was 38% to roots, 33% to the main shoot (excluding the first main shoot leaf), and nearly 30% to all tillers. Thus, when ^{14}C-herbicide was applied to the main shoot leaf, any translocated-[^{14}C]imazamethabenz was better allocated over the whole plant than when it was applied to the first leaf of the T1 tiller. The greater translocation to the roots, found when [^{14}C]imazamethabenz was applied to the first main shoot leaf, may have a profound inhibitory effect on whole plant growth. This result also explains why equivalent amounts of imazamethabenz applied to the main shoot only produced better control on the whole plant than when applied to the whole plant (both main shoot and tiller) and why the least inhibitory effect on whole plant growth was observed when imazamethabenz was applied to T1 only.

When imazamethabenz was delivered to T1 only no significant reduction in the fresh weight of other tillers (T2 and T3) was observed (Table 4). This may explain why exposing tillers to spray solution did not significantly increase herbicide efficacy, in contrast to the results of Smith and Chow (1990). There was very little reduction in total tiller fresh weight (Tables 1 and 2) because of the very limited translocation of imazamethabenz from exposed tillers to other tillers. The immature tiller is a metabolic sink and relies on the nutrient supply from the main shoot or parent shoot (Lauer and Simmons 1985, 1988, Quinlan and Sagar 1962, Rawson and Hofstra 1969). Thus, imazamethabenz absorbed by such a tiller is unlikely to leave because its translocation out of a leaf is mainly with the mass flow of photoassimilates (Little and Shaner 1991). When a tiller has two expanded leaves, as was the case with T1 in the radioactive label study, it becomes more self-sufficient but normally does not yet export its photosynthetic products out of the tiller (Marshall and Sagar 1968). Thus, [^{14}C]imazamethabenz absorbed by the first leaf of T1 was poorly allocated to plant parts other than T1 compared with the labeled herbicide absorbed by the first main shoot leaf.

From efficacy measurements and the patterns of absorption and translocation of [^{14}C]imazamethabenz, we have found that (1) although the greater leaf area contributed by T0 and T1 may increase herbicide interception per plant, their existence also increased total shoot dry weight by a similar extent; (2) according to values at the termination of the experiment, application of imazamethabenz to plants at the three-leaf stage with two tillers reduced fresh weight in the main shoot, total tillers, and total shoots to about the same extent as imazamethabenz application to plants at the two-leaf stage without tillers; and (3) [^{14}C]imazamethabenz was more evenly translocated through the whole plant when ^{14}C-herbicide was applied to the first main shoot leaf rather than to the first leaf of T1. It is concluded that the presence of early tillers during herbicide application neither increased nor decreased imazamethabenz efficacy in wild oat.

Acknowledgments. We thank Cyanamid Canada Inc. for financial support and supplying imazamethabenz and [^{14}C]-imazamethabenz. We also acknowledge Judy Hume for technical assistance in radioactive study and Haisheng Xie for determination of projected leaf area with image analyzer.

References

Carlsson BÅ, Callaghan TV (1990) Programmed tiller differentiation, intraclonal density regulation and nutrient dynamics in *Carex bigelowii.* OIKOS 58:219–230

Casal JJ, Sanchez RA, Deregibus VA (1986) The effect of plant density on tillering: The involvement of R/FR ratio and the proportion of radiation intercepted per plant. Environ Exp Bot 26:365–371

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 (1994a) Influence of nutrient supply and plant growth regulators on phytotoxicity of imazamethabenz in wild oat (*Avena fatua* L.). J Plant Growth Regul 13:195–201

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

Deregibus DVA, Sanchez RA, Casal JJ, Trlica MJ (1985) Tillering responses to enrichment of red light beneath the canopy in a humid national grassland. J Appl Ecol 22:199–206

Harker KN, O'Sullivan PA (1991) Effect of imazamethabenz on green foxtail, tartary buckwheat, and wild oat at different growth stages. Can J Plant Sci 71:821–829

Hoagland DR, Arnon DI (1939) The water culture method of growing plants without soil. Circ Calif Agric Exp Stn 347, 32 pp

Hucl P, Baker RJ (1990) Effect of seeding depth and temperature on tillering characteristics of four spring wheat cultivars. Can J Plant Sci 70:409–417

Jewiss OR (1972) Tillering in grasses: Its significance and control. J Br Grassland Soc 27:65–82

Lauer JG, Simmons SR (1985) Photoassimilate partitioning of main shoot leaves in field-grown spring barley. Crop Sci 25:851–855

Lauer JG, Simmons SR (1988) Photoassimilate partioning by tillers and individual tiller leaves in field-grown spring barley. Crop Sci 28:279–282

Little DL, Shaner DL (1991) Absorption and translocation of the imazamethabenz herbicides. In: Shaner DL, O'Connor SL (eds) The imazamethabenz herbicides. CRC Press, Boca Raton, FL, pp 53–69

Marshall C, Sagar GR (1968) The interdependence of tillers in *Lolium multiflorum* Lam.: A quantitative assessment. J Exp Bot 19: 785–794

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

Morrison IN, Mayert TSH (1982) Wild oat control in wheat with AC 222,293. Expert Committee on Weeds, Res Rep 2:671

Quinlan JD, Sagar GR (1962) An autoradiographic study of the movement of ^{14}C-labeled assimilates in the developing wheat plant. Weed Res 2:264–273

Rawson HM, Hofstra G (1969) Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plant. Aust J Biol Sci 22:321–331

Simmons SR, Lauer JG (1986) Shoot photoassimilate partioning patterns during the tillering phase in spring barley (*Hordeum vulgare* L.). In: Cronshaw J, Lucas WJ, Giaquinta RT (eds) Phloem transport. Alan R Liss, New York, pp 519–526

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

Takahashi K (1991) Relationship between main stem and primary tillers in the position of lowest elongated internode of deepwater rice. Jap J Crop Sci 60:400–406

van Hoogstraten SD (1983) Field performance of AC 222,293 in Europe during 1982. Int Congr Plant Prot 10:583

Xie HS, Caldwell BC, Hsiao AI, Quick WA, Chao JF (1995) Spray deposition of fenoxaprop and imazamethabenz on wild oat (*Avena fatua*) as influenced by environmental factors. Weed Sci 43:179–183

Xie HS, Hsiao AI, Quick WA (1996) Influence of temperature and light intensity on absorption, translocation, and phytotoxicity of fenoxaprop-ethyl and imazamethabenz-methyl in *Avena fatua*. J Plant Growth Regul 15:57–62

Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stage of cereals. Weed Res 14:415–421