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Effect of moisture stress and glyphosate on adventitious shoot growth of Canada thistle (*Cirsium arvense*)

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The effect of reduced water availability on glyphosate efficacy and adventitious shoot growth in male and female clones of Canada thistle was studied. Water availability was regulated with polyethylene glycol (PEG) in hydroponically grown plants or by withholding water from soil-grown plants. In hydroponic media, there was 50% more adventitious shoot growth from male plants than from female plants. Both PEG and foliarly applied glyphosate reduced the number of adventitious shoots, regardless of gender. In soil, the same number of adventitious shoots formed on untreated male and female plants. However, when glyphosate was applied to plants growing under dry conditions, there was 75% more adventitious shoot growth from males than females. Distribution of glyphosate was similar in male and female plants. Approximately 23% of applied ^{14}C-glyphosate was transported throughout Canada thistle plants within 10 d of treatment regardless of gender or moisture condition. Gender differences in capacity for vegetative reproduction may alter the sex ratio of Canada thistle populations in the field following glyphosate application.

Nomenclature: Glyphosate, Canada thistle [*Cirsium arvense* (L.) Scop.] CIRAR.

Key words: Male and female clones, polyethylene glycol (PEG), perennial weed, regrowth, translocation, CIRAR.

Populations of Canada thistle are difficult to control because they reproduce from seed and from adventitious shoots arising from root buds. Growth of adventitious shoots and survival of Canada thistle following herbicide application varies with plant moisture status and ecotype (Hodgson 1970; Hunter and Smith 1972; Zimdahl et al. 1991). Foliar applications of glyphosate will kill shoots and portions of the root, but new shoots can emerge from surviving root segments (Lauridson et al. 1983; Tworkoski and Sterrett 1992). Suppression of such adventitious shoot growth may require root segmentation 10 d after glyphosate application (Carlson and Donald 1988). Although it is generally accepted that glyphosate controls Canada thistle best when it is actively growing in moist soil (Haderlie et al. 1987), the effects of plant water status on glyphosate translocation and subsequent adventitious shoot growth in Canada thistle are not clear. Moisture stress reduced foliar absorption and translocation of glyphosate to roots of Canada thistle grown in the greenhouse but did not decrease control in the field (Lauridson et al. 1983).

Plant water status may affect distribution of growth within a Canada thistle plant. Shoots compete more effectively than adventitious shoots for limited moisture, thereby inhibiting adventitious shoot growth (Hunter et al. 1985). Canada thistle roots elongated more under dry than well-irrigated field conditions (Lauridson et al. 1983). These observations have implications for herbicide efficacy. In some experiments, active adventitious shoot growth was shown to promote glyphosate translocation from leaves to roots and result in accumulation of glyphosate to lethal concentrations (Carlson and Donald 1988; Tworkoski and Sterrett 1987). Therefore, reduced adventitious shoot growth resulting from lack of water at the time of herbicide application may contribute to decreased control of Canada thistle.

With some dioecious perennial plants of semiarid habitats, gender segregation occurs along moisture gradients, with females more prevalent in moist sites (Freeman et al. 1976). Canada thistle is dioecious and is adapted to dry grasslands (Kloppenburg and Hall 1990; Moore 1975). Amor and Harris (1975) found differences in vegetative expansion of male and female Canada thistle clones under different grazing pressure in Australia, but soil moisture was not evaluated as a covariable. Others have found different responses among clones to herbicide treatments (Frank and Tworkoski 1994; Hodgson 1970) and between genders to water stress (Thomas 1992). Male clones of Canada thistle survived polyethylene glycol (PEG)-imposed moisture stress better than female clones, and it was hypothesized that male plants may be better adapted to dry environments (Thomas 1992). Harris (1968) proposed that male plants of the dioecious perennial red sorrel (*Rumex acetosella* L.) predominate in established communities because males can devote resources to competition that females must allocate to sexual reproduction. Little work has focused on gender differences when Canada thistle is exposed to combined environmental stresses such as drought and herbicide.

Increased knowledge of the effects of water stress on movement of a systemic herbicide and on adventitious shoot growth in each gender can provide insight to Canada thistle's adaptation in agroecosystems. The objectives of this experiment were to (1) describe survival and adventitious growth in male and female plants of Canada thistle under different moisture regimes, and (2) evaluate susceptibility to glyphosate of male and female Canada thistle grown under different moisture regimes.

Materials and Methods

Two types of greenhouse experiments were conducted. In the first, plants were grown hydroponically and moisture status was varied with PEG. In the second, plants were grown in soil and moisture status was varied by differential application of water.

Plants

Three male and three female clones of Canada thistle were collected in Frederick, MD (Frank and Tworkoski 1994). Individual clones were vegetatively propagated and allowed to flower so that gender was confirmed. Male and female clones of Canada thistle were propagated by planting 5-cm-long root cuttings in soil in spring and growing them under natural light in a greenhouse (760 μmol m^{-2} s^{-1} PAR; 27 $\pm$ 4 C). All plants were 4 wk old (approximately 9 cm tall with six to eight leaves) for each experiment. In these experiments, all shoots developed adventitiously from the root. For consistency during discussion, the original, single shoot was termed the shoot and later developing shoots were termed adventitious shoots. Adventitious shoots that emerged from soil during the experiment were classified as secondary shoots.

Adventitious Shoot Growth Following PEG-induced Water Stress and Glyphosate Application

Roots were washed free of soil, and each plant was placed in a 1-L opaque glass container with half-strength Hoagland's solution (Hoagland and Arnon 1950) and polyethylene glycol[1] at the following concentrations: 0, 50, 70, and 90 mM. In preliminary experiments, these concentrations changed leaf water potential of Canada thistle without causing shoot chlorosis or necrosis. Each container was aerated during the experiment. Water potential of hydroponic media and leaves was measured after 1 and 2 wk. Water potential of hydroponic media was measured with thermocouple psychrometers[2] and corroborated by freezing point depression.[3] One hundred microliters of hydroponic solution was added to a small disk of Whatman No. 1 filter paper that was placed in the psychrometer chamber for measurement. Leaf water potential was measured using a leaf disk subsample with thermocouple psychrometers.

Plants were removed from the hydroponic media after 2 wk and roots were rinsed, then planted in soil. Plants were grown with adequate water in a greenhouse for an additional 2 wk, then removed from the soil, and adventitious shoot growth and shoot injury were evaluated. Adventitious shoots were counted when a discernible shoot apex had emerged from the root at least 3 mm. Shoot injury was measured as the average of three visual estimates with 0 = no injury and 100 = dead plants. The experimental design was random with nine replications. The experiment was repeated.

A third hydroponic experiment was performed with the same procedures described above, with one difference. A commercial formulation of glyphosate was applied to half of the plants at 2 kg ai ha^{-1} (350 L ha^{-1} carrier; 140 kPa; 8002 TeeJet flat-fan nozzle[4]) in a moving nozzle spray chamber[5] 2 d after Canada thistle was transplanted to hydroponic media. Roots and hydroponic media were shielded. The experiment was randomized with nine replicates.

Adventitious Shoot Growth and Glyphosate Distribution Following Glyphosate Application and Water Stress in Soil

Four-week-old Canada thistle plants growing in 1-L pots filled with loam, sand, and peatmoss (1:1:1 ratio by volume) were exposed to one of two moisture regimes: well watered (approximately 150 ml water per day) and dry (approximately 15 ml water per day). Pots were weighed each day to determine the volume of water necessary to maintain the target water potential for each plant. Leaf water potential was measured for a separate set of plants (six of each gender) for each water regime to verify that leaf water potential was between -1.5 and -2.0 MPa for dry plants and more than -0.5 MPa for well-watered plants. After 10 d of the watering regimes, half the plants from each water–gender combination were sprayed with glyphosate (2 kg ai ha^{-1} as described for the hydroponic experiment) and the other half were sprayed with water only. Plants were maintained either well watered or dry for an additional 10 d after glyphosate application, then all plants were again well watered. Care was used in watering to avoid wetting foliage. Adventitious shoot growth and injury were measured as described above 10 d and 8 wk after glyphosate treatment. Three plants with the same herbicide, gender, and soil moisture combination served as an experimental unit to determine the percent of plants with living shoots, secondary shoots, and root buds.

Root buds were counted 8 wk after treatment. Roots were oven dried at 80 C and immersed in 85% lactic acid at 60 C for approximately 6 d to clear (O'Brien and McCully 1981). The dark areas were root buds, i.e., adventitious shoot growth meristems that had not emerged from the root surface (McIntyre and Hunter 1975). Darkened areas were counted using a dissecting microscope.

^{14}C-glyphosate (3.7 kBq, 1,924 TBq mmol^{-1})[6] was applied to selected plants in all gender–moisture combinations that received commercial formulation of glyphosate, to determine glyphosate absorption and translocation. After the nonradioactive glyphosate dried, 20 μl of water containing 1.850 kBq isopropyl amine salt of ^{14}C-glyphosate was applied to each of two leaves (donor leaves) as described previously (Tworkoski and Sterrett 1992). Treated leaves were adjacent to one another at the midpoint of the stem. Five plants (replicates) of each gender–moisture combination received ^{14}C-glyphosate. Plants were harvested 10 d after treatment. Treated leaves were rinsed with a 20-mL directed stream of water to remove unabsorbed glyphosate. Water was evaporated and residual ^{14}C was measured.[7] The plants were divided into ^{14}C-treated leaves; the rest of the shoot, roots, and adventitious shoots within 50 cm of the root collar (proximal roots and adventitious shoots, respectively); and roots and adventitious shoots greater than 50 cm from the root collar (distal roots and adventitious shoots, respectively). Plant parts were dried and combusted,[8] and ^{14}C was quantified by liquid scintillation spectroscopy. Average ^{14}C recovery was 105% with a standard deviation of 6%.

The design for the adventitious shoot growth experiment was a two by two by two factorial with gender, moisture, and herbicide as main effects. At least 12 replications were used. The design for the glyphosate distribution experiment was a two by two factorial with gender and moisture as the main effects. Five replications were used in this experiment. Both experiments were repeated. Data from all experiments

TABLE 1. Growth of female and male Canada thistle following hydroponic root treatments of polyethylene glycol (PEG).

Main effects	Dry weight			Number of adventitious shoots
	Shoot	Root	Adventitious shoot	
	g			
Gender				
Female	1.3	0.4	0.08	3.0
Male	1.4	0.4	0.11	4.5
LSD (0.05)[a]	NS	NS	0.02	0.8
PEG concentration[b] (mM)				
0	1.8	0.6	0.28	4.4
50	1.3	0.4	0.13	4.1
70	1.2	0.4	0.09	3.6
90	1.2	0.3	0.05	2.9
LSD (0.05)	0.2	0.1	0.03	1.1
Source		$P > F$		
Gender (G)	0.17	0.38	0.01	0.01
PEG (P)	0.01	0.01	0.01	0.01
Linear	0.01	0.01	0.02	0.01
$G \times P$	0.32	0.36	0.55	0.29

[a] Fisher's Protected LSD test at the 5% level of probability. NS designates not statistically different.

[b] PEG concentrations of 0, 50, 70, and 90 mM represent solution water potentials of −0.14, −0.71, −1.27, and −2.49 MPa, respectively, that imposed leaf water potentials of −0.16, −0.90, −1.29, and −2.60 MPa, respectively.

were subjected to analysis of variance and mean separation using Fisher's Protected LSD test at the 0.05 probability level. Pearson correlation coefficients were calculated between adventitious shoot growth and shoot and root weight within a plant (SAS 1995).

Results and Discussion

Adventitious Shoot Growth Following PEG-induced Water Stress and Glyphosate Application

In the PEG experiments, male and female plants responded similarly to PEG; there were no gender-by-PEG or between-experiment interactions, so data from both experiments were pooled and main effects are presented (Table 1). Male plants produced 50% more adventitious shoots than female plants. Consequently, adventitious shoot dry weight also was greater in male plants, as the weight per adventitious shoot did not differ between genders. The difference in adventitious shoot growth between genders was not due to plant size. Shoot and root weights were the same for both genders.

Plants of both genders decreased in weight and adventitious shoot growth as PEG concentration increased (Table 1). Dry weights of shoots and roots decreased as PEG concentration increased from 0 to 50 mM, with no marked differences from 50 to 90 mM. In contrast, adventitious shoot dry weight decreased over the full range of PEG concentrations. This was likely due to shoots, and possibly roots, that dominate water capture and thus inhibit growth of adventitious shoots (Hunter et al. 1985; McIntyre 1979). Shoot injury associated with desiccation increased with increasing PEG concentration (data not shown). The lack of a significant gender-by-PEG interaction for adventitious shoot growth does not support Thomas' (1992) hypothesis that male plants were better adapted than female plants to a dry environment. Male plants had more adventitious shoot growth, regardless of moisture conditions. More resources may be available for vegetative reproduction in male plants because male flowers and pollen can require less energy than seed production in female plants. Male plants of red sorrel allocated a greater proportion of their resources to vegetative reproduction than female plants (Putwain and Harper 1972).

In the glyphosate experiment, no three-way interactions (herbicide-by-gender-by-PEG concentration) were found, but two-way interactions precluded averaging main effects. Glyphosate reduced the number of adventitious shoots and dry weights of roots and adventitious shoots (Table 2). A significant herbicide-by-gender interaction for adventitious shoot growth supports individual mean data that male plants produced more adventitious shoots than female plants when glyphosate was not applied. The only significantly larger number of adventitious shoots occurred with male plants that received no glyphosate. These results are similar to those of the first hydroponic experiments that indicated male plants grow more adventitious shoots than female plants.

Adventitious shoot number did not correlate with root dry weight or with shoot injury due to glyphosate ($r = 0.08$, $P > F = 0.52$, $n = 60$ and $r = -0.09$, $P > F = 0.46$, $n = 60$, respectively). Active adventitious shoot growth may increase basipetal translocation of foliar-applied systemic herbicides due to the strong sink activity within the root (Donald 1987; Tworkoski and Sterrett 1987). There was no indication that greater adventitious shoot growth capacity within male plants increased glyphosate efficacy; in fact, the adventitious shoot growth potential of male plants will likely increase survival of a male clone treated with glyphosate.

Adventitious Shoot Growth and Glyphosate Distribution Following Glyphosate Application and Water Stress in Soil

There were no treatment-by-experiment interactions, so data were combined from repeat experiments. Ten days after application, herbicide, moisture treatments, and gender had no effect on the number of plants with living shoots (data not shown). By 8 wk after application, glyphosate reduced the number of plants with living shoots in well-watered soil and root buds in dry and well-watered soil (Table 3). Although a shoot may have been injured, it was classified as alive if any living lateral shoot was present. Shoots of a few plants that received no glyphosate had flowered and senesced by the end of the experiment. Gender and moisture alone had no effect on survival of shoots or root buds. However, fewer shoots survived glyphosate treatment under well-watered than under dry conditions, validating the importance of soil moisture (Haderlie et al. 1987). Glyphosate had no effect on the number of plants with living secondary shoots (Table 3).

Glyphosate caused significant injury and, by 8 wk after treatment, it reduced weight of shoots and roots (Table 4). It also reduced the number of root buds but not the number of secondary shoots at the first or second harvest. By 8 wk

TABLE 2. Growth of female and male Canada thistle following hydroponic root treatments of polyethylene glycol (PEG) and foliar treatments of glyphosate.

Herbicide treatment	Gender	PEG concentration[a] (mM)	Dry weight: Shoot	Dry weight: Root	Dry weight: Adventitious shoot	Number of adventitious shoots
			g	g	g	
Glyphosate	Female	0	1.5	0.3	0.00	0.0
(2 kg ai ha^{-1})		50	1.5	0.4	0.03	0.5
		70	1.5	0.6	0.05	0.8
		90	1.3	0.3	0.00	0.0
	Male	0	1.7	0.4	0.02	1.4
		50	1.7	0.4	0.03	0.6
		70	1.7	0.5	0.06	0.9
		90	1.6	0.4	0.06	1.7
No glyphosate	Female	0	2.1	0.8	0.22	4.8
		50	2.0	0.8	0.29	4.5
		70	1.8	0.6	0.24	4.7
		90	1.4	0.4	0.12	4.1
	Male	0	2.5	0.9	0.33	9.1
		50	1.9	0.7	0.26	5.1
		70	1.8	0.5	0.23	6.2
		90	1.7	0.6	0.15	6.6
	LSD (0.05)[b]		0.6	0.2	0.08	2.1
Source				$P > F$		
Herbicide (H)			0.01	0.01	0.01	0.01
Gender (G)			0.11	0.91	0.04	0.01
PEG (P)			0.01	0.04	0.01	0.10
Linear			0.01	0.04	0.02	0.21
H × G			0.52	0.72	0.45	0.04
H × P			0.11	0.01	0.01	0.19
G × P			0.64	0.18	0.24	0.01
H × G × P			0.70	0.90	0.93	0.30

[a]PEG concentrations of 0, 50, 70, and 90 mM represent solution water potentials of −0.14, −0.83, −1.46, and −2.35 MPa, respectively, that imposed leaf water potentials of −0.19, −0.98, −1.44, and −2.3 MPa, respectively.
[b] Fisher's Protected LSD test at the 5% level of probability.

TABLE 3. Percent of female and male Canada thistle with living primary and secondary shoots and root buds in dry and well-watered soil 8 wk after foliar treatments of glyphosate.

Herbicide treatment	Gender	Soil moisture[a]	Survival: Shoot[c]	Survival: Secondary shoot	Survival: Root buds
			%	%	%
Glyphosate	Female	Dry	50	100	14
(2 kg ai ha^{-1})		Well-watered	0	79	0
	Male	Dry	31	92	23
		Well-watered	27	80	0
No glyphosate	Female	Dry	61	67	67
		Well-watered	100	100	75
	Male	Dry	75	100	92
		Well-watered	83	92	83
	LSD (0.05)[b]		32	25	27

[a] Soil moisture was maintained for 20 d by adding water to pots based on gravimetric measurements. At herbicide treatment (10 d after start of moisture treatments), dry and well-watered plant leaf water potentials were −1.30 and −0.49 MPa, respectively.
[b] Fisher's Protected LSD test at the 5% level of probability.
[c] Shoots were single original shoots that received glyphosate treatment. Secondary shoots were adventitious shoots that emerged from the soil after glyphosate treatment.

after treatment, there were more secondary shoots from plants receiving glyphosate. These secondary shoots must not have received toxic levels of glyphosate, and their number increased when the shoot was injured or killed.

As in the hydroponic experiments, male Canada thistle plants produced more adventitious shoots than females. The vegetative growth differential between male and female plants has potential ramifications for sexual reproduction within Canada thistle populations. All root buds will not develop as secondary shoots (Donald 1987), but if an equal proportion of male and female shoots are killed by glyphosate and an equal proportion of root buds survive and grow, then a shift in gender density to predominantly male populations will occur. Consequently, production of viable seed may decline.

Soil moisture and gender had a small effect on herbicide absorption (Table 5). Well-watered soil increased glyphosate absorption by Canada thistle, with more ^{14}C-glyphosate being translocated to the shoot but not to roots. Decreased absorption of glyphosate in water-stressed plants probably resulted from decreased diffusion through thickened, dehydrated cuticles (Kloppenburg and Hall 1990). Soil moisture had no effect on root glyphosate content or on glyphosate distribution throughout the root (data not shown). ^{14}C-glyphosate was uniformly distributed through the root system and the shoot, each containing an average of 17 and 6% of the absorbed glyphosate, respectively (Table 5). On average,

Table 4. Injury and growth of female and male Canada thistle in dry and well-watered soil 10 d and 8 wk after foliar treatment with glyphosate.

Time after treatment	Herbicide treatment	Gender	Soil moisture[b]	Injury[c] (%)	Dry weight: Shoot[d]	Dry weight: Root	Dry weight: Secondary shoot	Number: Secondary shoot	Number: Root buds
					g				
10 d	Glyphosate (2 kg ai ha^{-1})	Female	Dry	90	1.7	1.7	0.01	0.5	5.2
			Well-watered	85	2.0	2.0	0.02	0.6	4.9
		Male	Dry	87	1.8	1.9	0.16	2.9	5.3
			Well-watered	87	1.6	2.2	0.06	2.4	8.5
	No glyphosate	Female	Dry	6	1.7	2.1	0.12	1.1	10.9
			Well-watered	0	2.8	3.4	0.36	1.5	9.8
		Male	Dry	8	1.4	1.8	0.03	1.5	12.3
			Well-watered	0	2.1	3.5	0.13	3.3	18.5
	LSD (0.05)			5	0.2	0.2	0.08	1.0	2.4
8 wk	Glyphosate	Female	Dry	86	1.4	0.9	0.4	12.9	3.1
			Well-watered	84	1.7	1.0	0.5	18.6	5.4
		Male	Dry	83	1.9	1.4	0.9	22.7	3.7
			Well-watered	86	2.0	1.1	0.8	22.7	6.6
	No glyphosate	Female	Dry	8	3.7	4.7	0.6	6.2	13.2
			Well-watered	2	3.2	6.1	0.6	5.3	19.8
		Male	Dry	8	3.2	4.8	1.6	8.3	15.8
			Well-watered	0	3.7	6.6	1.4	13.0	20.3
	LSD (0.05)[a]			5	0.3	0.5	0.2	2.8	2.4

[a] Fisher's Protected LSD test at the 5% level of probability.
[b] Soil moisture was maintained for 20 d by adding water to pots based on gravimetric measurements. At herbicide treatment (10 d after start of moisture treatments), dry and well-watered plant leaf water potentials were −1.30 and −0.49 MPa, respectively.
[c] Averaged visual estimate of three people where 0 = no injury and 100 = a dead plant.
[d] Shoots were single original shoots that received glyphosate treatment. Secondary shoots were adventitious shoots that emerged from the soil after glyphosate treatment. Root buds were adventituous shoots that had not emerged from the root surface.

5% of absorbed ^{14}C-glyphosate was in roots within 50 cm from the root collar, and 12% was in roots more than 50 cm from the root collar. Less than 0.25% of absorbed glyphosate was in adventitious shoots, explaining the high survival rate of secondary shoots (Table 3). Male Canada thistle absorbed more glyphosate than female, but there were no gender differences in ^{14}C-glyphosate translocation and distribution.

Table 5. ^{14}C-glyphosate absorption and distribution in female and male Canada thistle in dry and well-watered soil 10 d after foliar treatments of glyphosate.

Main effects	Absorbed	Translocated	Distribution of absorbed glyphosate: Donor[c]	Shoot	Root
	% applied	% absorbed			
Soil moisture[a]					
Dry	89	21	79	5	16
Well-watered	91	25	75	7	17
LSD (0.05)[b]	1	NS	NS	1	NS
Gender					
Female	89	26	74	7	19
Male	91	20	80	6	15
LSD (0.05)	1	NS	NS	NS	NS

[a] Soil moisture was maintained for 20 d by adding water to pots based on gravimetric measurements. At herbicide treatment (10 d after start of moisture treatments), dry and well-watered plant leaf water potentials were −1.30 and −0.49 MPa, respectively.
[b] Fisher's Protected LSD test at the 5% level of probability. NS designates not statistically different.
[c] Donor leaves were two leaves per plant that received ^{14}C-glyphosate.

Glyphosate killed Canada thistle shoots present at the time of spraying. Shoot death likely released root buds and adventitious shoots from inhibition by apical dominance. Thus, glyphosate caused a redirection of water flow throughout the entire plant from larger to smaller shoots.

These experiments demonstrate a difference between male and female Canada thistle response to moisture stress and glyphosate. Male plants had more adventitious shoots than female plants when grown in hydroponic media (Tables 1 and 2). This difference occurred with or without foliar applications of glyphosate. These differences were not as consistent in soil-grown Canada thistle. In soil, males and females had the same number of adventitious shoots under the two moisture regimes when glyphosate was not applied (Table 4). However, when glyphosate was applied, more secondary shoots grew from males than females under drier conditions.

Under the stress conditions imposed in this experiment, it appears that more adventitious shoots can be produced by male than female Canada thistle plants. This difference in adventitious shoot growth potential did not alter the pattern or quantity of glyphosate that was translocated. Control was not affected by gender. However, the difference between genders in capacity for vegetative reproduction was evident under the combined stresses of glyphosate and reduced water. These findings indicate that with combined herbicide and water stress, the sex ratio of Canada thistle populations may be altered in the field, which may reduce the production of ovaries available for fertilization and seed. This possibility remains to be tested in the field.

Sources of Materials

[1] Polyethylene glycol, PEG 3350, Sigma, St. Louis, MO 63178.

[2] Thermocouple psychrometers, J.R.D. Merrill, Logan, UT 84321.

[3] Freezing point depression, Osmette S Automatic Osmometer Model 4002, Precision Systems Inc., Sudbury, MA 01776.

[4] 8002 TeeJet flat-fan nozzle, Spraying Systems Co., North Avenue, Wheaton, IL 60188.

[5] Moving nozzle spray chamber, Richard Scientific, Inc., 250 Bel Marin Keys Building, Suite D3, Navajo, CA 94949.

[6] ^{14}C-glyphosate, Sigma, St. Louis, MO 63178.

[7] Beckman 5801 scintillation counter, Irvine, CA 92713.

[8] Packard Tricarb oxidizer, Downers Grove, IL 60515.

Literature Cited

Amor, R. L. and R. V. Harris. 1975. Seedling establishment and vegetative spread of *Cirsium arvense* (L.) Scop. in Victoria, Australia. Weed Res. 15:407–411.

Carlson, S. J. and W. W. Donald. 1988. Glyphosate effects on Canada thistle (*Cirsium arvense*) roots, root buds, and shoots. Weed Res. 28: 37–45.

Donald, W. W. 1987. Effect of soil-applied chlorsulfuron on Canada thistle (*Cirsium arvense*) root and root bud growth. Weed Technol. 1:154–161.

Frank, J. R. and T. J. Tworkoski. 1994. Response of Canada thistle (*Cirsium arvense*) and leafy spurge (*Euphorbia esula*) clones to chlorsulfuron, clopyralid, and glyphosate. Weed Technol. 8:565–571.

Freeman, D. C., L. G. Klikoff, and K. T. Harper. 1976. Differential resource utilization by the sexes of dioecious plants. Science 193:597–599.

Haderlie, L. C., S. Dewey, and D. Kidder. 1987. Canada Thistle Biology and Control. Moscow, ID: University of Idaho Bull. 666. 7 p.

Harris, W. 1968. Environmental effects on the sex ratio of *Rumex acetosella* L. Proc. N. Z. Ecol. Soc. 15:51–54.

Hoagland, D. R. and D. I. Arnon. 1950. The Water Culture Method for Growing Plants Without Soil. Berkeley, CA: University of California Agricultural Experiment Station Circ. 347.

Hodgson, J. M. 1970. The response of Canada thistle ecotypes to 2,4-D, amitrole, and intensive cultivation. Weed Sci. 18:253–255.

Hunter, J. H., A. I. Hsiao, and G. I. McIntyre. 1985. Some effects of humidity on the growth and development of *Cirsium arvense*. Bot. Gaz. 146:483–488.

Hunter, J. H. and L. W. Smith. 1972. Environment and herbicide effects on Canada thistle ecotypes. Weed Sci. 20:163–167.

Kloppenburg, C. J. and J. C. Hall. 1990. Effects of formulation and environment on absorption and translocation of clopyralid in *Cirsium arvense* (L.) Scop. and *Polygonum convolvulus* L. Weed Res. 30:9–20.

Lauridson, T. C., R. G. Wilson, and L. C. Haderlie. 1983. Effect of moisture stress on Canada thistle (*Cirsium arvense*) control. Weed Sci. 31: 674–680.

McIntyre, G. I. 1979. Developmental studies on *Euphorbia esula*. Evidence of competition for water as a factor in the mechanism of root bud inhibition. Can. J. Bot. 57:2572–2581.

McIntyre, G. I. and J. H. Hunter. 1975. Some effects of the nitrogen supply on growth and development of *Cirsium arvense*. Can. J. Bot. 53:3012–3021.

Moore, R. J. 1975. The biology of Canadian weeds. 13. *Cirsium arvense* (L.) Scop. Can. J. Plant Sci. 55:1033–1048.

O'Brien, T. P. and M. E. McCully. 1981. The Study of Plant Structure. Principles and Selected Methods. Melbourne, Australia: Termarcarphi. Pp. 6.14–6.18.

Putwain, P. D. and J. L. Harper. 1972. Studies in dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosa* and *R. Acetosella*. J. Ecol. 60:113–129.

[SAS] Statistical Analysis Systems. 1995. SAS Procedures Guide. Version 6.11. Cary, NC: Statistical Analysis Systems Institute.

Thomas, R. F. 1992. The Effect of Temperature on Infection of Canada Thistle by *Puccinia punctiformis* and the Influence of Infection and Moisture Availability on Reproduction in Canada Thistle. M.A. thesis. Hood College, Frederick, MD. 43 p.

Tworkoski, T. J. and J. P. Sterrett. 1987. Modification of root bud growth in Canada thistle with selected plant growth regulators: effects on translocation of glyphosate. J. Plant Growth Regul. 6:221–232.

Tworkoski, T. J. and J. P. Sterrett. 1992. Phytotoxic effects, regrowth, and ^{14}C-sucrose translocation in Canada thistle treated with mefluidide, flurprimidol, and systemic herbicides. J. Plant Growth Regul. 11:105–111.

Zimdahl, R. L., J. Lin, and A. A. Dall'Armellina. 1991. Effect of light, watering frequency, and chlorsulfuron on Canada thistle (*Cirsium arvense*). Weed Sci. 39:590–594.

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