Plant Physiol. (1990) 93, 1441–1448
0032-0889/90/93/1441/08/$01.00/0

Received for publication September 8, 1989
Accepted March 3, 1990

Herbicide Chlorsulfuron Decreases Assimilate Transport Out of Treated Leaves of Field Pennycress (*Thlaspi arvense* L.) Seedlings[1]

Hank D. Bestman*[2], Malcolm D. Devine[3], and William H. Vanden Born

Department of Plant Science, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5

ABSTRACT

Treatment of field pennycress (*Thlaspi arvense* L.) leaves with the herbicide chlorsulfuron resulted in a decrease in the export of assimilate. Twelve hours after a spot application of 1 microgram, assimilate translocation was 70% of that in control leaves. In excised leaves treated with chlorsulfuron the total amounts of sugars and free amino acids were 150 and 170%, respectively, of the amounts in control leaves, 30 hours after herbicide treatment. The amount of sucrose was 247% of that in control leaves. The increase in the concentration of sucrose in the chlorsulfuron-treated leaves, combined with the absence of an effect of chlorsulfuron on carbon dioxide fixation, suggests that the decrease in assimilate transport is not due to an effect on the synthesis of assimilates, but rather to an effect on their movement out of the leaves. Supplying branched-chain amino acids to the field pennycress seedlings prior to the application of chlorsulfuron prevented the occurrence of the effects described.

The herbicidal action of a chemical arises from its ability to interact with a plant in such a manner as to inhibit or disturb its growth. This interaction usually involves the inhibition of a process essential to growth. The sulfonylurea herbicide chlorsulfuron[4] inhibits the growth of susceptible plants by inhibiting the enzyme ALS, an enzyme common to the biosynthesis of the branched-chain amino acids L-valine, L-leucine, L-isoleucine (4).

In order for a postemergence herbicide to provide successful control of a deep-rooted perennial weed, for example, Canada thistle (*Cirsium arvense* [L.] Scop.), it must be translocated from the foliage to the roots following spray application. Sweetser et al. (23) have reported that 2 to 28% of the applied dose was translocated out of treated leaves of several species in a 24-h period. Export of less than 5% of the absorbed chlorsulfuron in 24 h has been reported for Canada thistle and perennial sow thistle (*Sonchus arvensis*) (8) and for Tartary buckwheat (*Fagopyrum tataricum* [L.] Gaertn.) (2).

The limited phloem mobility of chlorsulfuron cannot be explained in terms of the ability of plant tissue to accumulate the herbicide (6, 7) but, instead, is attributed to an effect on assimilate translocation. The objective of the research described in this paper was to understand the effect of chlorsulfuron on the translocation of assimilates out of treated leaf tissue of field pennycress (*Thlaspi arvense* L.) seedlings. In addition, the rates of uptake and of translocation of the herbicide and the extent of its metabolism were determined.

MATERIALS AND METHODS

Plant Material

Field pennycress (*Thlaspi arvense* L.) seedlings were grown from seed in 175-mL styrofoam cups filled with horticultural-grade vermiculite. The cups were subirrigated with half-strength Hoagland solution (15) modified to contain 1.5 μg/mL iron. The plants were grown in a growth cabinet at 23°C/19°C day/night temperatures and with an 18-h photoperiod. Fluorescent lights supplied a photosynthetic photon flux density of 800 $\mu E \cdot m^{-2} \cdot s^{-1}$. The RH was 50%.

In experiments that included the branched-chain amino acids L-valine, L-leucine, and L-isoleucine, these amino acids were supplied to the seedlings via the roots. Six to 8 h before herbicide treatment the vermiculite was washed off the roots and the seedlings were mounted with styrofoam plugs in holes in a sheet of PVC (6 mm thick) in such a manner that the roots were hanging in half-strength Hoagland solution, with or without 1-mM concentrations of each of the three amino acids.

Herbicide Application

Chlorsulfuron, ^{14}C-labeled (phenyl-^{14}C [U]; specific activity 152.1 $Bq.nmol^{-1}$; radiochemical purity 98.9%) or technical product (95% pure), was applied in 8 to 10 droplets (total volume 10 μL) of application solution consisting of 10 mM Na_2HPO_4-citric acid buffer (pH 8.0), with 10% (v/v) tetrahydrofuran and 0.1% (v/v) Citowett Plus surfactant. The droplets were placed on the third true leaf of seedlings that had five to seven true leaves. Control treatments consisted of 8 to

[1] Research funded by the Natural Sciences and Engineering Research Council of Canada. H. D. B. was the recipient of a Dissertation Fellowship of the University of Alberta.

[2] Present address: The King's College, 10766-97 Street, Edmonton, Alberta, Canada. T5H 2M1.

[3] Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, S7N 0W0.

[4] Abbreviations: chlorsulfuron, 2-chloro-*N*-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]-carbonyl]benzenesulfonamide; ALS, acetolactate synthase (EC 4.1.3.18); LSS, liquid scintillation spectrometry; MCW, methanol:chloroform:water 12:5:3 (v/v/v); imazapyr, (±)-2-[4,5-dihydroxy-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid.

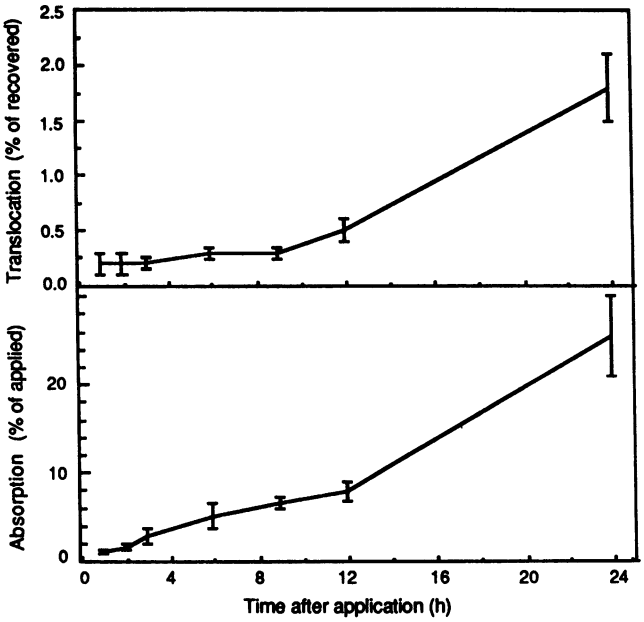

Figure 1. Absorption and translocation of [^{14}C]chlorsulfuron in field pennycress seedlings. The data, means and standard errors, are the results of two runs with three seedlings per treatment. 'Recovered' radioactivity includes surface wash and all radioactivity in the tissue.

10 droplets (10 μL total volume) of application solution without chlorsulfuron.

Assimilation Chamber

The $^{14}CO_2$-labeling experiments were conducted in a custom-built circular assimilation chamber that could accommodate up to six intact field pennycress seedlings in such a manner that the roots, a single leaf of each seedling, and the remaining parts of the shoots were in three completely separate compartments (24). Sealing between the inner compartment and the outer compartment, and between the outer compartment and the root compartment, was done with a cellulose filler around the stems and the petioles. Hydrocarbon-free air of known CO_2 concentration was supplied independently to the single-leaf compartment and the shoot compartment at a rate that maintained a CO_2 concentration of 400 ± 25 μL/L within each compartment. The roots of the seedlings were immersed in 15 mL nutrient solution. The entire chamber was placed in a temperature-controlled water bath at 25 ± 0.5°C. Incandescent and fluorescent lights supplied a photosynthetic photon flux density of 300 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the level of the seedlings in the chamber. The RH in the chamber was 40%.

$^{14}CO_2$-Labeling

$^{14}CO_2$ was generated from [^{14}C]$NaHCO_3$ and lactic acid outside the chamber, and was circulated via a peristaltic pump through a closed loop connected with the appropriate compartment. During the 30-min labeling period the CO_2 concentration within the compartment was kept constant by pumping a sodium bicarbonate solution into the lactic acid at a rate equivalent to the net rate of CO_2 incorporation by the plants. In all instances, the plants incorporated more than 95% of the ^{14}C activity supplied. During a subsequent chase period, hydrocarbon-free air of known CO_2 concentration was supplied as described earlier.

Assimilate Movement in Intact Seedlings

Six uniform seedlings were placed in the assimilation chamber. After an 8-h dark period, followed by 2 h light, 1 μg chlorsulfuron was applied to the third leaf of three of the seedlings, in 8 to 10 droplets as for the radiolabeled chlorsulfuron. Leaves of the other three seedlings were treated with application solution without herbicide. Within the chamber, control plants and herbicide-treated plants were arranged in an alternating pattern. $^{14}CO_2$ (185 kBq) was supplied 6, 12, or 24 h after herbicide treatment, for a 30-min labeling period followed by a 90-min chase period. The seedlings were then removed from the chamber and fresh weights of the treated leaves, the shoots, and the roots were determined. The plant parts were stored at −20°C until they were combusted in a biological sample oxidizer. Radioactivity was quantified by standard LSS. For each run, data from the herbicide-treated plants were expressed as percentages of the data from control plants.

Absorption and Translocation of Chlorsulfuron

Seedlings were harvested 1, 2, 3, 6, 9, 12, or 24 h after the application of 500 Bq [^{14}C]chlorsulfuron. The amount of herbicide on the leaf surface at harvest time was determined

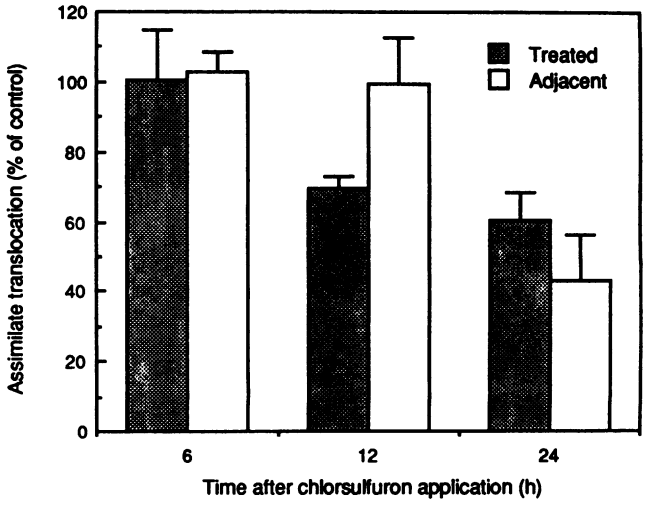

Figure 2. Effect of 1 μg chlorsulfuron, applied to a single leaf of intact field pennycress seedlings, on the translocation of ^{14}C assimilates out of the treated leaf, or out of an adjacent untreated leaf. Leaves were exposed to $^{14}CO_2$ (30 min pulse, 90 min chase period) 6, 12, or 24 h after herbicide application. The data are expressed as a percentage of controls, and are based on the results of three runs with three seedlings per treatment. Bars on the graph represent standard errors.

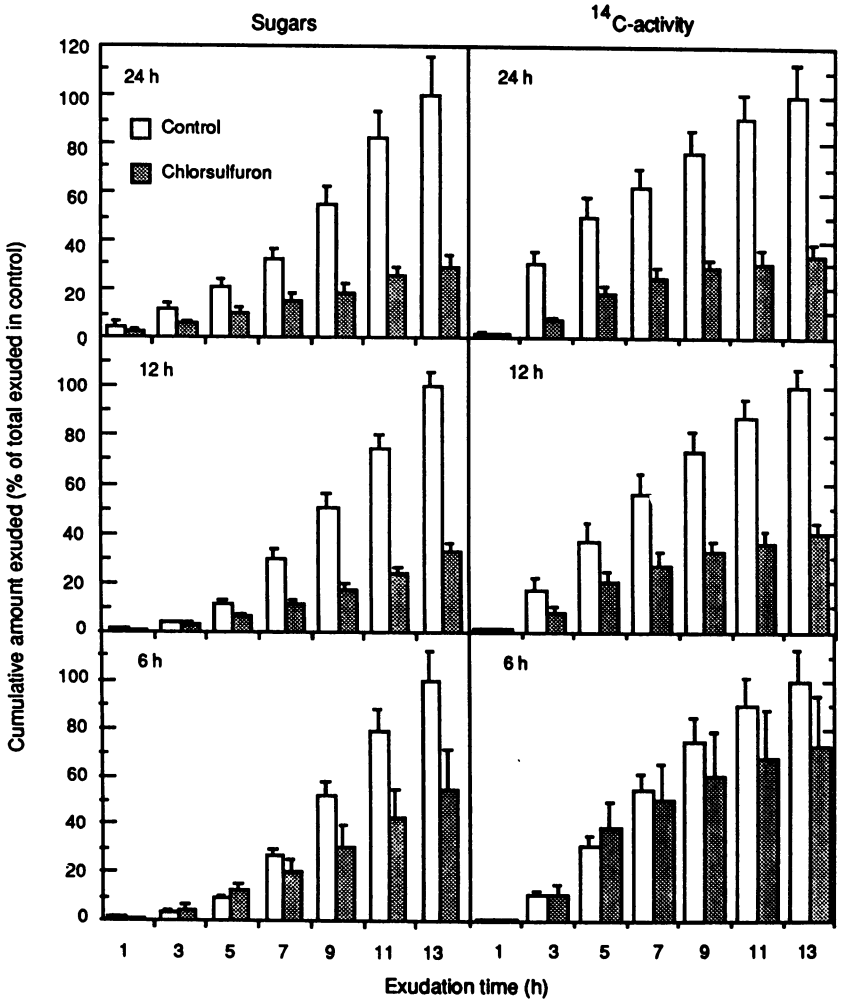

Figure 3. Exudation profiles of excised field pennycress leaves treated with 0 or 1 μg of chlorsulfuron, excised, and exposed to $^{14}CO_2$ (30 min pulse) 6, 12, or 24 h later. The data, means, and standard errors, are expressed as percentages of the cumulative total amount of ^{14}C activity or sugars exuded by control leaves during the exudation period, and are the results of two runs with three leaves per herbicide dose.

Table I. *Effect of Chlorsulfuron on Assimilation and Exudation by Excised Leaves of Field Pennycress Seedlings, and Allocation of ^{14}C Activity in Sugar and Amino Acid Fractions Extracted from These Leaves following Exposure to $^{14}CO_2$*

The leaves were excised and exposed to $^{14}CO_2$ (30 min pulse; 330 min chase period) 24 h after the application of 0 (blank) or 1 μg of chlorsulfuron. The data are mean results of two runs with three leaves per treatment.

Parameter and Fraction	Units[a]	Chlorsulfuron		Herbicide Effect as Percentage of Control[b]	
		Blank	1 μg		
Assimilation					
^{14}C activity assimilated	dpm mg^{-1}	31,759	33,943	104	NS[b]
Exudation					
Total ^{14}C activity	dpm mg^{-1}	1,477	763	50	**
Total sugars	nmol mg^{-1}	2.02	1.06	53	**
Leaf extracts					
Sugars					
Total sugar	nmol mg^{-1}	34.0	49.4	150	*
Total ^{14}C activity	dpm mg^{-1}	12,891	21,353	163	*
Specific activity	dpm $nmol^{-1}$	381	436	108	NS
Amino acids					
Total amino acids	nmol mg^{-1}	16.8	28.6	170	**
Total ^{14}C activity	dpm mg^{-1}	2,245	2,315	105	NS
Specific activity	dpm $nmol^{-1}$	138	88	64	**

[a] Weights (mg) refer to tissue fresh weights. [b] NS, not significant; * significant at $P \leq 0.05$; ** significant at $P \leq 0.01$.

by rinsing the treated leaf three times with 5 mL 10% (v/v) ethanol (5). Total radioactivity in the rinse solutions was quantified by LSS. The vermiculite was washed off the roots and the plants were divided into four parts, i.e., roots, treated leaf, shoot apex, and the remaining part of the shoot. The plant parts were stored at −20°C until they were combusted.

Metabolism of Chlorsulfuron

The extent of chlorsulfuron metabolism in seedlings was determined (3) 12 or 24 h after application of 500 Bq [^{14}C]-chlorsulfuron. Plants were ground twice in deionized water, the homogenate then was centrifuged (10,000 *g*, 10 min) and filtered. Protein was removed by precipitation with cold acetone and further centrifugation (1,000 *g*, 10 min). The acetone was evaporated, the remaining extract was lyophilized, and the dried residue was dissolved in 1 mL deionized water. Chlorsulfuron and its metabolites were separated by loading an aliquot of the extract on a C_{18} reverse-phase preparative chromatography column and were eluted with a water/methanol (with 0.1% [v/v] formic acid) step gradient. Only the fraction that was eluted at 45% (v/v) methanol contained unmetabolized chlorsulfuron.

Exudation of Assimilate by Excised Leaves

Six 1.5-mL centrifuge tubes were installed in the inner compartment of the assimilation chamber. Each tube was connected with a line to a 5-mL syringe outside of the chamber. Excised leaves (petioles recut under water), treated with 0 or 1 μg of chlorsulfuron, were placed with their petioles in the tubes containing a 5 mM phosphate buffer (pH 6.0) with 0.5 mM EDTA (10, 13, 16). The CO_2 concentration in the chamber was maintained at 400 μL/L. $^{14}CO_2$ was applied for 30 min at 6, 12, or 24 h after the herbicide treatment. The bathing solution was changed 1, 3, 5, 7, 9, 11, and 13 h after the start of the $^{14}CO_2$ application. The solutions containing the exudates were put in culture tubes and weighed. A 700-μL aliquot was taken for the determination of ^{14}C activity by LSS. The amount of sugar in the exudates was determined by an anthrone-based colorimetric method (22). The data were expressed as percentages of the appropriate controls.

Exudation of Assimilates following Application of [^{3}H]- and [^{14}C]Sucrose

The third leaf of field pennycress seedlings was treated with 0 or 1 μg of chlorsulfuron. The treatments were applied to a 1-cm^2 oval-shaped area on the adaxial surface of the leaves. Twelve or 24 h later, the treated leaves were excised and placed with their petioles in 1.5-mL centrifuge tubes containing 0.5 M phosphate buffer (pH 6.0) with 0.5 mM EDTA. [^{14}C]-Sucrose was applied to the area of the leaf that had been treated with chlorsulfuron, and [^{3}H]sucrose was applied to the area of the leaf that had been treated with blank application solution. The bathing solution was changed 2, 4, 6, 8, 10, and 12 h after the application of the radiolabeled sucrose.

Twelve h after application of the radiolabeled sucrose the leaves were washed with 10% ethanol to remove unabsorbed sucrose (5). The leaves were frozen with liquid nitrogen and stored at −20°C until they were combusted in a biological sample oxidizer.

Incorporation of ^{14}C into Excised Leaves

Leaves were excised and exposed to $^{14}CO_2$ (185 kBq), 24 h after treatment with 0 or 1 μg chlorsulfuron. Following a 30-min labeling period and a 330-min chase period the leaves were frozen with liquid nitrogen and stored at −20°C.

Extraction of Leaf Tissue

The various fractions were extracted according to a procedure adapted from Dickson (9). The tissue was homogenized in MCW. Following a phase separation, the upper water-alcohol phase was transferred to a boiling flask and reduced to dryness under vacuum. The residue was dissolved in 1 mL water and stored at −20°C.

Fractionation of the Water-Alcohol Fraction

The water-alcohol fraction was fractionated using an ion exchange chromatography method (1). The whole fraction was loaded on a cation exchange column (4.5 mL; Dowex 50X8-400; hydrogen form) connected in series with an anion

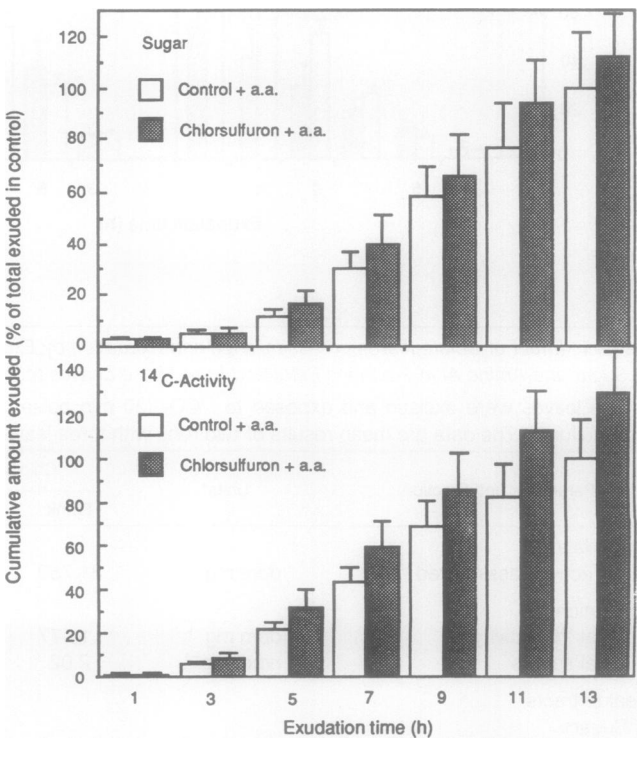

Figure 4. Exudation profiles of excised field pennycress leaves treated with 0 or 1 μg chlorsulfuron, excised, and exposed to $^{14}CO_2$ (30 min pulse) 6, 12, or 24 h later. Six to 8 h before herbicide application the seedlings were placed with their roots in half-strength Hoagland solution containing 1 mM L-valine, L-leucine, and L-isoleucine. The data, means, and standard errors are expressed as percentages of the cumulative total amount of ^{14}C activity or sugars exuded by control leaves during the exudation period, and are the results of two runs with three leaves per herbicide dose.

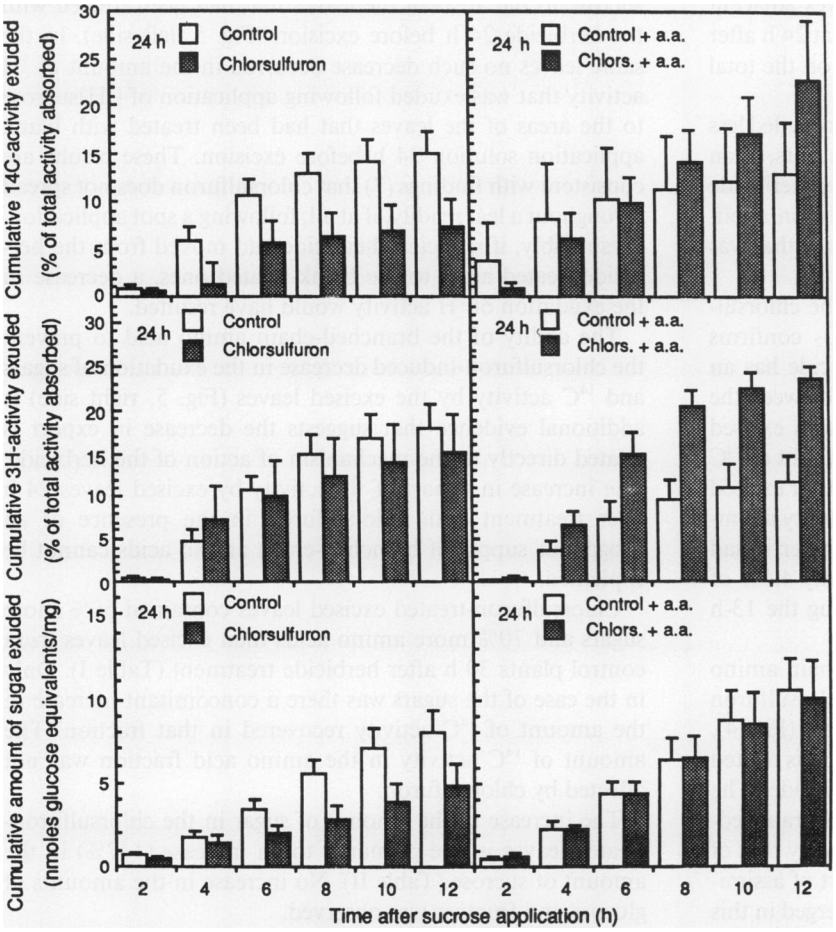

Figure 5. Exudation profiles of excised field pennycress leaves treated with 0 or 1 μg of chlorsulfuron 24 h before treatment with [^{3}H]- and [^{14}C]sucrose. Six to 8 h before herbicide application the seedlings were placed with their roots in half-strength Hoagland solution or in half-strength Hoagland solution containing 1 mM L-valine, L-leucine, and L-isoleucine. [^{14}C]Sucrose was applied to the area of the leaf that had been treated with herbicide; [^{3}H]sucrose was applied to the area that had not been treated with herbicide. The data, means, and standard errors are expressed as nanomoles of glucose equivalents exuded per mg of tissue, or as the cumulative amount of ^{3}H or ^{14}C activity exuded as a percentage of the total activity absorbed; they are the results of one run with six leaves per herbicide dose.

exchange column (4.5 mL; Dowex 1X8-400; formate form). The neutral fraction, containing the sugars, was eluted with 20 mL water. The columns then were disconnected and the amino acid fraction was eluted from the cation exchange column with 60 mL of 3 N HCl. The remaining sugars were eluted from the anion exchange column with an additional 10 mL water. All eluents were reduced to dryness at 40°C. The residues were dissolved in 1 mL water and stored at −20°C.

Analysis of the Sugar Fraction

The total amount of sugar in this fraction was determined colorimetrically (22) and total radioactivity was determined by LSS. The individual sugars were separated by HPLC (300 × 7.8 mm Aminex HPX-87H column; ambient temperature; 20-μL sample loop; 0.01 N H_2SO_4 mobile phase; 0.8 mL/min flow rate; refractive index detection). They were collected in scintillation vials and ^{14}C activity in each was determined by LSS.

Analysis of the Amino Acid Fraction

The total amount of amino acids in this fraction was determined according to the method outlined by Moore (18). All samples were assayed in duplicate.

RESULTS AND DISCUSSION

Fate of Chlorsulfuron

Chlorsulfuron was absorbed and translocated slowly (Fig. 1). Twenty-four hours after application of 3.3 nmol of chlorsulfuron, 2.4 nmol of herbicide were recovered in the leaf washes and 0.8 nmol were recovered from the tissue. Only 0.05 nmol were translocated out of the treated leaf. Total recovery was 97%. Due to the low specific activity of the radiolabeled chlorsulfuron and the small amount of chlorsulfuron exported to the shoot apical tissue, the amount of herbicide present in that tissue could not be determined accurately.

Chlorsulfuron was metabolized very slowly. At 24 h after application of ^{14}C-labeled chlorsulfuron, 90% of the extractable ^{14}C activity was associated with unmetabolized chlorsulfuron. In the metabolism experiments, on average, 92% of the absorbed ^{14}C activity was extracted, and 93% of the applied activity was recovered.

Assimilate Transport

Intact leaves of chlorsulfuron-treated seedlings exported only 60 to 70% of the amount of ^{14}C assimilates exported by intact leaves of control plants 12 or 24 h after herbicide treatment (Fig. 2). No such effect was observed 6 h after

herbicide treatment. Export of assimilate by leaves adjacent to the herbicide-treated leaves was decreased only at 24 h after herbicide treatment. Chlorsulfuron had no effect on the total amount of $^{14}CO_2$ assimilated by the plants.

Excised leaves of chlorsulfuron-treated seedlings exuded less assimilate, both in terms of ^{14}C activity and sugars, than excised leaves of control plants 12 or 24 h after herbicide treatment (Fig. 3; Table I). At 6 h after chlorsulfuron application, only a decrease in the total amount of sugars that was exuded was observed.

The decrease in the export of ^{14}C activity by the chlorsulfuron-treated leaves following exposure to $^{14}CO_2$ confirms previous findings (7) that indicate that the herbicide has an effect on assimilate translocation. The agreement between the results obtained with intact seedlings and those with excised leaves occurred despite large differences in the amount of ^{14}C activity translocated or exuded in the control plants or excised leaves. In intact seedlings, 16% of the total ^{14}C activity assimilated was translocated out of the third leaf, 2 h after it had been exposed to $^{14}CO_2$. Excised leaves exuded only 4.6% of the total amount of ^{14}C activity assimilated during the 13-h period following exposure to $^{14}CO_2$.

In intact seedlings treated with the branched-chain amino acids L-valine, L-leucine, and L-isoleucine, chlorsulfuron caused little or no decrease in assimilate transport (Fig. 4). This suggests that the decrease in assimilate transport is related directly to the mechanism of action of the herbicide. The details of how the inhibition of the biosynthesis of branched-chain amino acids, and as a consequence presumably that of proteins, is related to the decrease in the transport of assimilates out of the herbicide-treated leaf have not emerged in this study. One possibility is that the effect on assimilate translocation may be associated with the depletion of proteins involved in the transport of sucrose into the phloem.

The effect of chlorsulfuron on the assimilate transport system is restricted to a localized area close to where the herbicide is applied and enters the leaf. Chlorsulfuron decreased the amount of ^{14}C activity and reducing sugars that was exuded by excised leaves following application of [^{14}C]-sucrose to the areas of the leaves that had been treated with the herbicide 24 h before excision (Fig. 5, left side). In the same leaves no such decrease occurred in the amount of ^{3}H activity that was exuded following application of [^{3}H]sucrose to the areas of the leaves that had been treated with blank application solution 24 h before excision. These results are consistent with findings (7) that chlorsulfuron does not spread throughout a leaf readily, if at all, following a spot application. Presumably, if sufficient herbicide had moved from the herbicide-treated areas to the blank-treated ones, a decrease in the exudation of ^{3}H activity would have resulted.

The ability of the branched-chain amino acid to prevent the chlorsulfuron-induced decrease in the exudation of sugars and ^{14}C activity by the excised leaves (Fig. 5, right side) is additional evidence that suggests the decrease in export is related directly to the mechanism of action of the herbicide. The increase in export of ^{3}H activity by excised leaves 24 h after treatment with chlorsulfuron in the presence of an exogenous supply of branched-chain amino acids cannot be explained.

Chlorsulfuron-treated excised leaves contained 50% more sugars and 70% more amino acids then excised leaves from control plants 30 h after herbicide treatment (Table I). Only in the case of the sugars was there a concomitant increase in the amount of ^{14}C activity recovered in that fraction. The amount of ^{14}C activity in the amino acid fraction was not affected by chlorsulfuron.

The increase in the amount of sugar in the chlorsulfuron-treated leaves is due primarily to an increase (147%) in the amount of sucrose (Table II). No increase in the amounts of glucose and fructose was observed.

The increase in the concentration of sugars, particularly sucrose, in the treated leaves indicates that the effect of chlorsulfuron is not first of all an effect on the synthesis of sugars, but more likely on their transport into the phloem. This increase in sugars in herbicide-treated leaves has also been reported for imazapyr (21), an imidazolinone-type herbicide known to inhibit ALS (20). On the basis of the mass flow hypothesis of phloem transport, it can be assumed that

Table II. *Effect of Chlorsulfuron on the Amounts of Sucrose, Glucose, and Fructose and Their Specific Activities following Exposure of Excised Field Pennycress Leaves to $^{14}CO_2$*

The leaves were excised and exposed to $^{14}CO_2$ (30 min pulse; 330 min chase period) 24 h after the application of 0 (blank) or 1 μg of chlorsulfuron. The data are mean results of two runs with three leaves per treatment.

Sugar and Parameter	Units[a]	Chlorsulfuron		Herbicide Effect as Percentage of Control[b]	
		Blank	1 μg		
Sucrose					
Total amount	nmol mg^{-1}	1.7	4.2	247	*
Specific activity	dpm $nmol^{-1}$	1,021	734	75	NS
Glucose					
Total amount	nmol mg^{-1}	11.9	16.0	144	NS
Specific activity	dpm $nmol^{-1}$	369	408	102	NS
Fructose					
Total amount	nmol mg^{-1}	5.7	7.4	140	NS
Specific activity	dpm $nmol^{-1}$	557	739	127	**

[a] Weights (mg) refer to tissue fresh weights. [b] NS, not significant; * significant at $P \leq 0.05$; ** significant at $P \leq 0.01$.

once the sucrose has been loaded into the phloem tissue, it should be translocated, unless there is an effect on the unloading in the sink tissue, or there is an obstruction in the phloem between source and sink (6, 11). The fact that the chlorsulfuron-induced decrease in assimilate transport also occurs in excised leaves strongly suggests that the herbicide has an effect on the transport of assimilates into the phloem in the source tissue rather than an effect in the sink tissue.

The effect of chlorsulfuron on assimilate translocation appears to be mediated differently than the one caused by glyphosate, a herbicide also reported to decrease phloem transport (11). The decrease induced by glyphosate is due to a decrease in the net carbon exchange rate, which is attributed to a decrease in the concentration of ribulose bisphosphate (12, 19). The absence of an effect of chlorsulfuron on the total amount of $^{14}CO_2$ assimilated by the treated leaves suggests that in the time period studied (up to 24 h) in these experiments, the herbicide had no measurable effect on photosynthesis. This confirms earlier reports (14). The accumulation of sucrose in chlorsulfuron-treated leaf tissue suggests an effect analogous to that of *p*-chloromercuribenzenesulfonic acid, which inhibits the loading of sucrose into the phloem (17).

Concomitant with the increase in sugars in chlorsulfuron-treated leaf tissue is an increase in the concentration of amino acids. Both the size of the pools of the individual amino acids (or of groups of biosynthetically related amino acids), and the flux of carbon atoms through them are under metabolic control. We postulate that a decrease in the biosynthesis of one group of amino acids, *i.e.* the branched-chain amino acids, might not necessarily result in an immediate decrease in the total amount of amino acids in the leaf tissue. On the contrary, a decrease in the synthesis of the branched-chain amino acids might first of all result in a decrease in protein synthesis, due to a lack of availability of these amino acids. This decrease in protein synthesis might result in an accumulation of amino acids other than the branched-chain ones. The overall effect could be an increase in the total amount of amino acids in the tissue. In the absence of data on the composition of the amino acid fractions and on the total amount of ^{14}C activity incorporated in each amino acid, the details of the effect of chlorsulfuron on amino acid metabolism in field pennycress leaves remain speculative.

One of the consequences of chlorsulfuron-induced decrease in the rate of assimilate transport out of the treated leaves is a decrease in the rate at which the herbicide molecules themselves are translocated out of the treated tissue (11). Devine *et al.* (6) have suggested that on the basis of its physical-chemical properties chlorsulfuron should be translocated more readily than it is in whole plants. Assuming that chlorsulfuron has no direct effect on the loading of herbicide molecules into the phloem tissue, *i.e.* an effect not mediated through the inhibition of branched-chain amino acid biosynthesis, supplying the treated plant with branched-chain amino acids should increase the rate of chlorsulfuron transport.

The decrease in the export of assimilates out of leaves of field pennycress seedlings in which the synthesis of branched-chain amino acids has been inhibited by the herbicide chlorsulfuron suggests a close link between the continued availability and/or synthesis of these amino acids and assimilate export. The nature of this link remains to be determined.

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