Plant Physiol. (1987) 85, 82–86
0032-0889/87/85/0082/05/$01.00/0

Uptake and Accumulation of the Herbicides Chlorsulfuron and Clopyralid in Excised Pea Root Tissue[1]

Received for publication January 21, 1987 and in revised form May 15, 1987

MALCOLM D. DEVINE*, HANK D. BESTMAN[2], AND WILLIAM H. VANDEN BORN
Department of Plant Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5

ABSTRACT

The herbicides chlorsulfuron and clopyralid were taken up rapidly by excised pea root tissue and accumulated in the tissue to concentrations ten and four times those in the external medium, respectively. Uptake was related linearly to external herbicide concentration over a wide concentration range, implying that transport across the membrane is by nonfacilitated diffusion. Uptake of both compounds was influenced by pH, with greatest uptake at low pH. The pH dependence of uptake suggests that the herbicides (both of which are weak acids) are transported across the plasma membrane in the undissociated form, and accumulate in the cytoplasm by an ion trap mechanism. Most of the absorbed herbicide effluxed from the tissue when it was transferred to herbicide-free buffer, indicating that the accumulation was not due to irreversible binding. Consequently, both herbicides remain available for transfer to the phloem. These results can explain the high reported phloem mobility of clopyralid in intact plants. The low phloem mobility of chlorsulfuron must be accounted for by factors that override its ability to accumulate in the symplast.

There has been considerable interest in recent years in the mechanisms by which plant growth regulating chemicals, both natural and synthetic, move across cell membranes. In the case of naturally occurring compounds this interest has been directed towards determining the way(s) in which concentrations of these compounds, at both the tissue and cellular levels, are regulated by the plant. Results indicate that endogenous plant growth-regulating chemicals are transported across membranes by both nonfacilitated and carrier-mediated processes (1, 17). Endogenous control of the latter process presumably plays a role in regulating internal concentrations.

Herbicide uptake into plant tissue has been studied primarily in relation to the subsequent translocation of the herbicides. Herbicide entry and retention in the symplast are prerequisites for phloem transport (19, 26), and the relationship between phloem transport and physicochemical properties of herbicides has been the focus of much attention recently (6, 19).

The herbicides chlorsulfuron and clopyralid[3] are used for the control of certain broadleaf weeds, including Canada thistle (*Cirsium arvense* [L.] Scop.) and perennial sowthistle (*Sonchus arvensis* L.). Clopyralid is much more phloem-mobile than chlorsulfuron in both species (9). The research described in this paper was conducted to determine if the observed difference in phloem mobility could be explained on the basis of differential uptake and/or accumulation in plant tissue.

MATERIALS AND METHODS

Plant Material. Pea (*Pisum sativum* L. cv Homesteader) seeds were germinated in vermiculite in the dark at 25°C. Five d after planting, the seedlings were harvested and 1-cm apical root sections were cut off and rinsed in tap water. These were subsequently blotted dry, and approximately 500 mg (fresh weight) of roots (about 60 individual root tips) were weighed into glass scintillation vials containing 3.0 ml buffer (0.1 M citrate-phosphate, pH 5.4).

Absorption in Live and Dead Tissue. The experimental approach used in this research was similar to that described by Peterson and Edgington (20). Herbicide absorption was determined by monitoring the disappearance of ^{14}C-labeled herbicide from the bathing solution over a 4-h period. Chlorsulfuron ([U-^{14}C]phenyl; 152 Bq·nmol^{-1}) and clopyralid ([^{14}C]2,6-pyridinyl; 429 Bq·nmol^{-1}) were prepared in solutions of distilled water:ethanol (9:1, v/v) so that the final herbicide concentration, when 10 μl of these solutions was added to 3.0 ml buffer, was 1.0 μM. The ^{14}C content of the solutions was measured by taking a 50-μl aliquot at specified time intervals (including $t = 0$, immediately after the herbicide was added) and assaying for ^{14}C by LSS. Absorption was calculated by correcting the ^{14}C data for the fraction of total solution assayed, with appropriate adjustment for the change in solution volume, and was expressed as picomoles of herbicide absorbed/100 mg root tissue.

Absorption was measured in fresh pea root tissue and in tissue that had been killed by immersion in liquid N_2. The root tips were weighed into glass vials and liquid N_2 was added so that the root tips were completely covered for at least 30 s. The tissue was then thawed by immersing the vials in trays of warm water. This procedure was carried out three times on all samples. Although vitality of the tissue was not checked, it was assumed that this procedure killed the tissue. The ratio of herbicide concentration in the tissue to that in the bathing solution (C_i/C_o) was also calculated, assuming the tissue and the solution to be of equal density.

Release of Absorbed Herbicide upon Freezing. Pea root tips were allowed to take up herbicide as described above. After 4 h the vials were removed from the shaker and the tissue was killed by immersion in liquid N_2. The vials were replaced on the shaker for 15 min, at which time 50 μl aliquots were taken and assayed by LSS. Herbicide content of the tissue, and C_i/C_o values, were obtained using these data.

pH Dependence. Herbicide absorption was measured in root

[1] Research funded by the Natural Sciences and Engineering Research Council of Canada.

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

[3] Abbreviations: chlorsulfuron, 2-chloro-*N*-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzenesulfonamide; clopyralid, 3,6-dichloropyridinecarboxylic acid; 2,4-D, 2,4-dichlorophenoxyacetic acid; GA_1, gibberellin A_1; LSS, liquid scintillation spectrometry; MCPA, (4-chloro-2-methylphenoxy)acetic acid; CPMU, *N*-(*p*-carboxyphenyl)-*N'*-methylurea.

tips placed in solutions that ranged in pH from 3.4 to 6.4, using a series of citrate-phosphate buffers (0.1 M). Measurement of the pH at the end of the experiments indicated that the solution pH did not change by more than 0.2 units during the 4-h uptake period.

Herbicide Concentration Dependence. Citrate-phosphate buffers (0.1 M, pH 5.4) were prepared with unlabeled herbicide at appropriate concentrations so that, when the ^{14}C-labeled herbicide was added, the final herbicide concentrations were 1, 10, 10^2, and 10^3 μM. Absorption of ^{14}C was then measured over a 4-h period. Total herbicide absorption was calculated on the basis of the ^{14}C taken up by the tissue and the specific activities of the different treatment solutions.

Elution Experiments. Elution of herbicide from the tissue was measured by allowing the tissue to take up herbicide for 4 h, then removing the remaining herbicide-containing solution by vacuum filtration and replacing it with 3.0 ml herbicide-free buffer. In the continuous elution experiments this 3.0 ml was used to rinse the root tips for approximately 20 s; it was then removed and replaced with 3.0 ml fresh buffer. The ^{14}C content of the bathing solution was monitored over time as described above. Stepwise elution was measured by replacing the bathing solution with fresh buffer every 5 min until 15 such transfers had been completed. The buffer removed at each transfer was added directly to a scintillation vial and assayed for ^{14}C content by LSS. The amount of ^{14}C remaining in the tissue at the end of these experiments was determined by difference, based on the ^{14}C content of the bathing solutions as previously described, and also by assaying the root tips for ^{14}C. This was done by transferring the root tips to small porcelain boats and combusting them in a biological sample oxidizer (model OX300, R. J. Harvey Instrument Corp., Hillsdale, NJ). The released $^{14}CO_2$ was trapped and collected in a mixture of trapping reagent (organic base) and scintillation liquid, and ^{14}C content was determined by LSS.

All experiments were conducted at 22 ± 2°C, and the vials were shaken on a laboratory shaker at 120 rpm throughout the experiments. Each experiment consisted of three replicate vials per treatment, and all experiments were conducted at least twice. The results of one representative experiment are reported in each instance. Confidence limits are not shown in the figures, but standard errors were seldom greater than 5% of the treatment means.

Determination of Partition Coefficients. Partition coefficients (P) of the two herbicides between n-octanol and pH 5.4 citrate-phosphate buffer (0.1 M) were determined experimentally by adding ^{14}C-herbicide to premixed equal volumes of n-octanol and buffer, and shaking for 120 min. The containers were then centrifuged and the ^{14}C content in each fraction was assayed by LSS (18). This method, while not providing absolute P values, does provide reliable estimates of comparative lipophilicity.

RESULTS

Absorption in Live and Dead Tissue. Chlorsulfuron was absorbed more rapidly and more completely than clopyralid in the fresh pea root tissue. For both herbicides, uptake reached a maximum after 2 to 3 h (Fig. 1). Uptake into the tissue that had been killed by freezing proceeded quickly initially but leveled off after approximately 15 min, and increased only slowly for the duration of the experiment. Both herbicides accumulated inside the tissue against a concentration gradient. Chlorsulfuron and clopyralid reached a C_i/C_o of 1.0 after approximately 10 and 30 min, respectively, in the live tissue, and values of approximately 10 and 4.5 were reached after 4 h. After 4 h, concentrations of both herbicides in the dead tissue were slightly higher than the external concentrations (2.1 and 1.7 for chlorsulfuron and clopyralid, respectively).

Release of Absorbed Herbicide upon Freezing. Freezing the tissue after a 4-h uptake period resulted in release of most of the absorbed herbicide from the tissue to the bathing solution. The resultant C_i/C_o values were 1.1 for chlorsulfuron, and 1.0 for clopyralid.

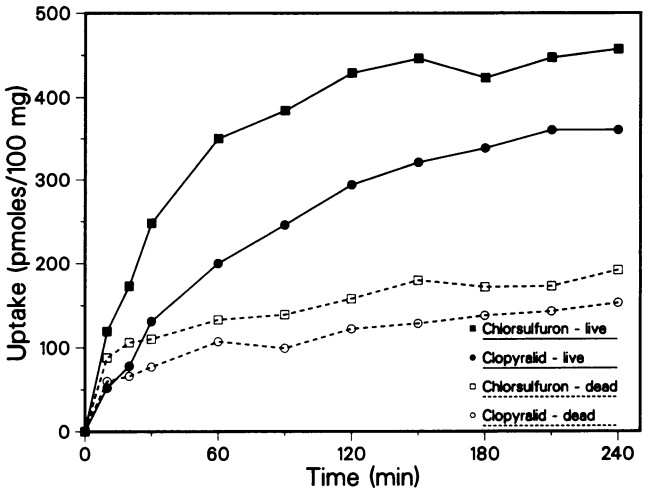

FIG. 1. Time course of chlorsulfuron and clopyralid uptake in pea root tissue. The bathing solution was 0.1 M citrate-phosphate buffer (pH 5.4). Initial herbicide concentration was 1.0 μM. The root tissue was freshly excised root tips (10 mm); dead tissue was killed by immersion in liquid N_2, then rinsed prior to treatment.

pH Dependence. Uptake of both herbicides was influenced markedly by the pH of the bathing solution, with greatest uptake at low pH (Fig. 2, A and B). This relationship was especially clear in the pH range 4.4 to 6.4. Uptake at pH 3.4 initially was greater than at the higher pH values, but leveled off between 30 and 60 min, and at the end of the experiments was lower than uptake at pH 4.4.

Herbicide Concentration Dependence. Herbicide uptake was related linearly to external concentration over a wide concentration range (Fig. 3). The data shown are for a 30-min uptake period, but similar plots were obtained for longer uptake periods (not shown). The extremely high r^2 values obtained by least square linear regression analysis suggest that the straight lines shown represent the best possible description of the data.

Elution Experiments. The two herbicides eluted from the tissue quite readily upon transfer to herbicide-free buffer (Fig. 4A). Elution was more rapid in the case of the stepwise transfers, in which the 15 transfers were completed in 75 min (Fig. 4B). Herbicide efflux in the continuous efflux experiment would be complete when equilibrium was reached between the herbicide in the tissue and that in the bathing solution. At equilibrium the C_i/C_o values should be equal to those at the end of the uptake period. In fact, the end-point C_i/C_o values were slightly lower than those reached after 4 h of uptake, suggesting that the system was at, or close to, equilibrium. Efflux in the stepwise elution experiment would be complete only when all of the available herbicide had been removed from the tissue, but both herbicides continued to elute from the tissue up to the 15th transfer (Fig. 4B). Given the small amount of herbicide eluted in the final transfer, and the relatively large amount remaining in the tissue, C_i/C_o values for the final transfer were very large (75 and 73 for chlorsulfuron and clopyralid, respectively). It remains to be seen how much of the herbicide remaining in the tissue would have been eluted had the experiment been extended. Regardless, it is clear that most of the absorbed herbicide was available for transfer to the phloem.

Determination of Partition Coefficients. P values obtained were 1.3 for chlorsulfuron and 0.0018 for clopyralid (mean of five separate determinations for each herbicide). This indicates that chlorsulfuron is much more lipophilic than clopyralid at this pH.

DISCUSSION

The results in Figure 1 indicate that both chlorsulfuron and clopyralid can be taken up readily by pea root tissue, and can accumulate to levels well above the external concentration. The very large reduction in herbicide accumulation in killed root tissue suggests that accumulation of these herbicides in pea roots is associated with metabolic function and the presence of an intact plasma membrane. Freezing probably ruptured the plasmalemma and, consequently, accumulation via a membrane-associated mechanism would not be expected to occur. Presumably, accumulation is associated with the trans-membrane pH gradient generated by membrane-bound, proton-pumping ATPases. Further experiments using metabolic inhibitors or different temperatures might better define the particular metabolic processes involved in this accumulation. Peterson and Edgington (20) described the release of 2,4-D from potato tuber discs that were frozen after they had been allowed to take up the herbicide for 90 min. This resulted in a C_i/C_o = 1.0 (termed '100% tissue volume penetration' in their paper). In unfrozen tissue, 2,4-D accumulated to a C_i/C_o value of approximately 16. The release of most of the absorbed herbicide in our experiments when the tissue was frozen following 4 h of uptake further supports the contention that intact membranes are required for accumulation of the herbicides in this tissue. These observations are in contrast to those made on the uptake of atrazine, a neutral, lipophilic herbicide, in barley roots (28). Equal uptake of atrazine was observed in live and dead tissue, suggesting no direct membrane involvement in uptake or accumulation. The slight accu-

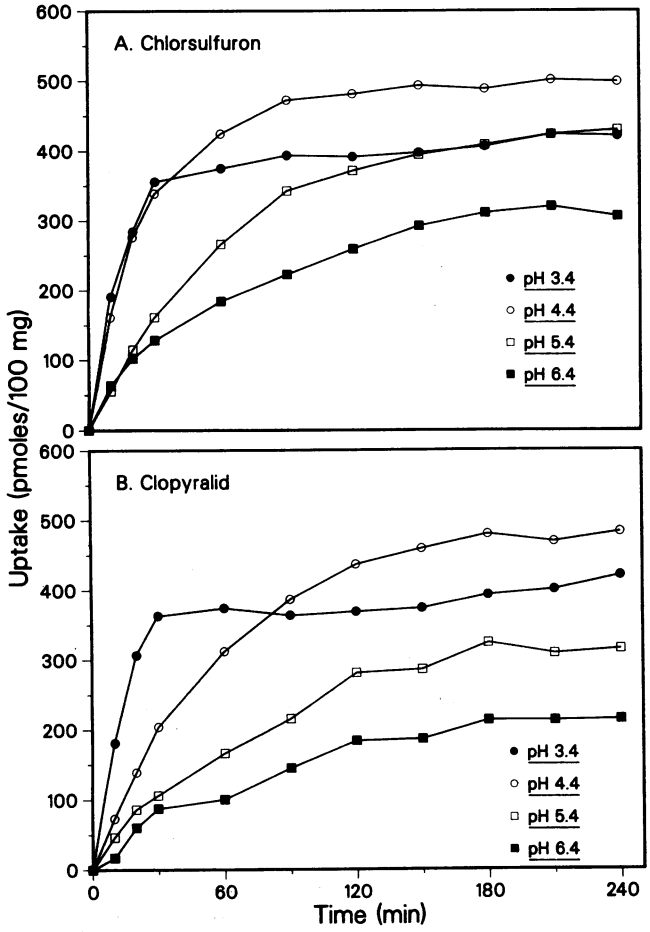

FIG. 2. pH dependence of uptake of chlorsulfuron (A) and clopyralid (B) in pea root tissue. Bathing solutions were citrate-phosphate buffer (pH 3.4, 4.4, 5.4, and 6.4). Additional details as in Figure 1.

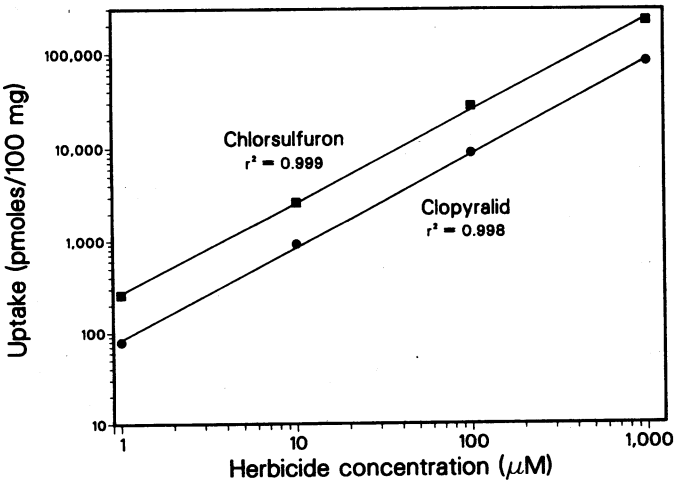

FIG. 3. Concentration dependence of uptake of chlorsulfuron and clopyralid in pea root tissue over the range 1 to 10^3 μM. Fitted lines were obtained by least square linear regression analysis. The data shown are for a 30-min uptake period.

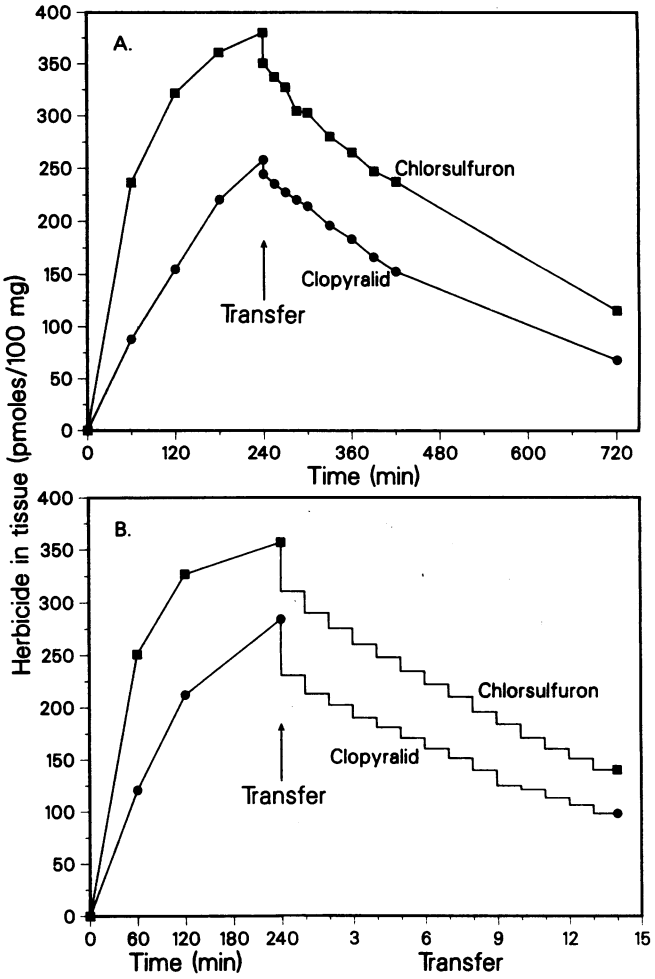

FIG. 4. Efflux of chlorsulfuron and clopyralid from pea root tissue following uptake for 4 h. A, Continuous efflux into fresh buffer following a 20-s rinse; B, stepwise efflux obtained by repeated transfers of the roots to fresh buffer at 5-min intervals. Note that the scale in (B) changes from time in minutes to number of transfers. See "Materials and Methods" for additional details.

mulation of chlorsulfuron and clopyralid in tissue killed by freezing suggests that some binding may have occurred in or on the tissue.

Penetration of xenobiotics into plant cells is governed largely by their lipophilicity; more lipophilic compounds move into (or out of) the cytoplasm more rapidly (5, 24). The observed difference in P values provides a plausible explanation for the more rapid uptake of chlorsulfuron than clopyralid in these experiments.

Herbicides can accumulate in plant tissue by several mechanisms, including ion trapping of weak acids (7, 19, 20), partitioning into lipid fractions (5), binding to cellular components (2, 27), or by metabolic conversion to products less able to cross the plasmalemma (6). Chlorsulfuron and clopyralid are both weak acids (pK_a values of 3.6 and 2.3, respectively), and their accumulation in pea root tissue is consistent with weak acid accumulation. The ratio of undissociated to dissociated molecules in the external solution (calculated according to the Henderson-Hasselbach equation) is proportional to the solution pH, and the greater uptake at low pH (Fig. 2) suggests that the herbicides cross the plasmalemma as the undissociated acids. The leveling off of uptake at pH 3.4 after 30 to 60 min cannot be explained readily, but may reflect some effect of this low pH on the tissue itself. A pH-dependent uptake of several other classes of weakly acidic herbicides has been reported (7, 17, 20, 21). This pH dependence is analogous to that observed with the weakly acidic endogenous plant growth regulators IAA (11, 22), ABA (15), and GA_1 (18) in plant tissues, isolated cells, or membrane vesicles.

The absence of saturable kinetics in the uptake of both herbicides (Fig. 3) suggests that both herbicides are taken up by a passive, nonfacilitated process. These results are similar to those obtained for amitrole (16, 25), monuron (10), and napropamide (2). Some caution should be exercised in interpreting some of the published results, however, because the reported experiments have not always been conducted over a sufficiently wide concentration range to truly distinguish between a carrier-mediated and a nonfacilitated process. Evidence for carrier-mediated uptake of herbicides is restricted to 2,4-D (10, 17), which closely resembles the endogenous plant growth regulator IAA, and glyphosate (4), which may be transported on a phosphate carrier.

Most of the absorbed chlorsulfuron and clopyralid was eluted readily from within the tissue, indicating that their accumulation in the tissue is not due to strong binding. Although we did not identify the ^{14}C compounds eluted from or remaining in the tissue, it is very unlikely that metabolic conversion played a role in their accumulation. Neither herbicide is likely to be metabolized rapidly in susceptible species such as peas. Furthermore, both herbicides are metabolized to glycoside derivatives that are considerably more polar than the parent molecules (3; MD Devine, unpublished results), and it is unlikely that these metabolites would readily penetrate the plasma membrane.

The efflux profiles (Fig. 4) are similar to those reported previously for 2,4-D (20), MCPA (13), CPMU, and maleic hydrazide (14), all of which are phloem mobile or ambimobile. Although 2,4-D is considered to be a phloem-mobile herbicide, our previous research indicates that clopyralid is considerably more phloem-mobile than 2,4-D (compare data in Refs. 8 and 9). Efflux profiles for xylem-mobile herbicides differ greatly from those shown here. Several reports indicate much more rapid and more complete efflux of such herbicides (6, 13, 14, 20). One consequence of this rapid efflux is that, although such compounds may freely enter the symplast, they are readily lost to the apoplast and translocated in the xylem.

Phloem mobility of herbicides usually is explained on the basis of one of two hypotheses. Herbicides that are weak acids can enter the symplast and accumulate there by an ion trapping mechanism, based on the relatively low permeability of the plasma membrane to the dissociated species (17, 19). Herbicides retained in this manner are passed on to the phloem, and are translocated through the plant in that tissue. Alternatively, the herbicide may enter the cytoplasm slowly but, once inside, may be retained there because of the relatively low permeability of the membrane to the herbicide. This intermediate diffusion hypothesis has been used to explain the phloem mobility of glyphosate (12) and amitrole (16).

Clopyralid is extremely phloem-mobile, and in some species almost all of the clopyralid that is absorbed by a mature leaf can be exported from that leaf (9). Whereas one might predict, based on the above information and the data presented, that chlorsulfuron would be equally or even more mobile in the phloem, this is not the case. In fact, chlorsulfuron shows only limited phloem transport in several plant species (9; MD Devine, unpublished data). One possibility is that chlorsulfuron might leak out of the phloem and transfer into the xylem to a greater extent than clopyralid. This might be expected, because chlorsulfuron is considerably more lipophilic than clopyralid, and there is evidence in the literature to suggest that, up to a point, lipophilic compounds are translocated more readily in the xylem than are hydrophilic compounds (5, 23). If this did occur, more of the applied chlorsulfuron would be found at the tips and margins of treated leaves, *i.e.* distributed in a pattern consistent with apoplastic translocation. In other experiments, however, we have found that this is not the case, and that most of the absorbed chlorsulfuron is retained close to the site of entry into the leaf (data not shown).

The clopyralid data provide a satisfactory explanation for the observed phloem mobility of that herbicide, based on accumulation of the clopyralid anion in the cytoplasm. The fact that chlorsulfuron behaves similarly to clopyralid in excised tissue but not in whole plants indicates that weak acid accumulation does not necessarily impart phloem mobility to a herbicide. We are currently investigating the possibility of chlorsulfuron translocation being restricted by an effect of this herbicide on the process of phloem translocation itself.

Acknowledgments—Labeled chlorsulfuron and clopyralid were provided by E. I. du Pont de Nemours & Co. (Inc.) and Dow Chemical Co., respectively. The able technical assistance of Chris Bladen is gratefully acknowledged.

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