

Vernalization affects absorption and translocation of clopyralid and aminopyralid in rush skeletonweed (*Chondrilla juncea*)

Research Article

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Abstract

The developmental status of perennial weeds such as rush skeletonweed (*Chondrilla juncea* L.) can influence herbicide absorption and translocation. Differential efficacy between fall and spring applications suggests vernalization impacts herbicide absorption and translocation in other perennial asters. Clopyralid and aminopyralid absorption and translocation were quantified in nonvernalized and vernalized plants following application of ¹⁴C-labeled herbicides 2, 4, 8, 24, and 72 h after treatment. Less ¹⁴C clopyralid was absorbed, and at a slower rate, in vernalized plants. Movement out of the treated leaf was slower, with ¹⁴C clopyralid translocating more rapidly than ¹⁴C aminopyralid. More ¹⁴C moved to the roots in nonvernalized plants compared with vernalized plants, regardless of herbicide. Increased translocation to belowground survival structures is needed for effective control of *C. juncea*.

Introduction

Rush skeletonweed (*Chondrilla juncea* L.) is an important invasive perennial weed of southeastern Australia and the U.S. Pacific Northwest region (Heap 1993; McVean 1966). The center of origin for *C. juncea* is Eurasia, from northern Germany to central Russia between 35°N and 55°N (McVean 1966). *Chondrilla juncea* is most commonly found in pastures, non-crop areas, cereal cropland, and Conservation Reserve Program lands, where it competes for soil moisture and nutrients, interferes with harvesting, and reduces cereal grain yield by up to 80% (Cullen 1984; Heap 1993; Myers and Lipsett 1957). Not only is *C. juncea* apomictic, but it also readily undergoes vegetative reproduction through taproot and rhizome-like lateral roots with intense vigor (Rosenthal et al. 1968; Stebbins 1941). The development of a *C. juncea* plant from seed begins in the fall, following seed dispersal. Fall-emerging juvenile *C. juncea* plants consist of basal rosettes, which persist through winter vernalization to the spring, forming inflorescences by summer. Stem buds of the roots form from seed dispersal in fall until the initiation of the next year's inflorescence the following spring (Rosenthal et al. 1968).

Optimization of chemical control methods for management of *C. juncea* is difficult due to the recalcitrant biology and ecology of *C. juncea* plants (Jacobs et al. 2009). In particular, regeneration from distant root sections and apparent minimal translocation to the expansive root network are primary reasons why repeated herbicide applications are needed to obtain adequate control (Wallace and Prather 2008). There are also very limited herbicide options for management of *C. juncea*, including aminopyralid and clopyralid (Heap 1993; Jacobs et al. 2009; Van Vleet and Coombs 2012; Winston et al. 2009). Indeed, little information about absorption and translocation of herbicides is available for *C. juncea* and is limited to aminocyclopyrachlor (Bell et al. 2011). Both aminopyralid and clopyralid accumulate in the actively growing tissue, and so may be impacted by source–sink relationships (Raudenbush and Keeley 2014; Shaner 2014). Changes in the source–sink relationships over *C. juncea* developmental stages have been cited as a potential reason for its reduced translocation of 2,4-D (Greenham 1962).

One of the most important considerations for *C. juncea* management with aminopyralid and clopyralid is the direction of photosynthate flow to energy sinks. Perennial weeds often alternate sinks depending on environmental cues (Tworkoski 1992; Wilson et al. 2001). The environmental cue of vernalization occurs through a prolonged exposure to cold temperatures and initiates the process of flowering in many species (Kim et al. 2009). Vernalization controls other processes, such as cuticular wax production, vegetative vigor and reproduction, initiation of floral primordia, and release from dormancy (Chouard 1960; Kim et al. 2009; Rohde and Bhalerao 2007; Rosenthal et al. 1968). Changes due to vernalization in source–sink relationships of *C. juncea* have not previously been investigated. Other perennial weeds, like Canada thistle [*Cirsium arvense* (L.) Scop.], respond to environmental cues by modifying the source–sink relationship between the roots and shoots from fall to spring or after flowering (Tworkoski 1992; Wilson et al. 2006). *Cirsium arvense* roots serve as a sink from summer to early spring and a

source from early spring to summer. Increased translocation to the roots occurs from summer to fall before leveling off until spring, after which translocation of photoassimilates is predominately directed away from the roots to support the growing shoots (Hodgson 1968; Nkurunziza and Streibig 2011; Tworokoski 1992). The changes in source–sink competition contribute to higher levels of photoassimilate translocation to the roots in the fall (Tworokoski 1992). Correlating with the change in source–sink competition, control of *C. arvensis* with clopyralid applied in the fall is greater compared with spring applications (Wilson et al. 2006). The increase in efficacy corresponds to a disruption of seasonal changes in root sucrose reserves implicated in winter survival. Conversely, aminopyralid controls *C. arvensis* equally well in the fall and spring (Enloe et al. 2007). It is likely that similar processes are involved with source–sink regulation in *C. juncea*, but there is no information available addressing direction of photoassimilate flow before or after vernalization or absorption and translocation of aminopyralid or clopyralid. Therefore, the objective of this paper is to quantify the effect of vernalization on absorption or translocation of aminopyralid and clopyralid in *C. juncea*.

Materials and Methods

Plant Material and Experimental Conditions

Chondrilla juncea plants of similar size were harvested from a wheat field in LaCrosse, WA, in late fall of 2015 and 2016. The rhizomes were cut into 5-cm sections for planting in individual 15-cm pots containing Sunshine® grow mix L1 potting mix (Sun Gro Horticulture Distribution, 770 Silver Street, Agawam, MA 01001). Plants were grown for 3 wk in a growth chamber at 9-h daylength and 27 C. The plants were randomly placed into two groups of 50 plants. Before herbicide application, each group received either a vernalization treatment or no vernalization treatment. The vernalization treatment consisted of vernalization in a 4 C vernalization chamber with a 9-h photoperiod for 8 wk, followed by 1 wk of acclimation in the 27 C growth chamber before herbicide application. The nonvernalization treatment consisted of holding the plants in the 27 C growth chamber for 1 wk before treatment. Nonvernalized and vernalized plants were thus separated in age by 8 wk, though plant size was consistent between vernalization treatments.

Herbicide Application

The herbicide treatments were applied as an overspray application followed by a point treatment of either clopyralid (Stinger®, Dow Chemical, 9330 Zionsville Road, Indianapolis, IN 46268) or aminopyralid (Milestone®, Dow Chemical). The 210 g ai ha⁻¹ overspray application was applied to 25 plants, randomized from each group, using a syringe sprayer system. The syringe sprayer system consisted of an adjustable full cone sprayer nozzle with a syringe and aspirator. The system was adjusted to deliver 168 L ha⁻¹ by manual actuation of the syringe handle over 1 s. The youngest, completely unfurled leaf of each plant was covered with impermeable plastic before the overspray treatment. Immediately following the overspray treatment, the leaf was uncovered, and the point treatment was applied to the previously covered leaf surface. The point treatment consisted of 5 evenly spaced 0.5- μ l droplets of either [¹⁴C]aminopyralid (specific activity 3.3 kBq) (Dow Chemical Company) or [¹⁴C]clopyralid (specific activity 3.3 kBq) (Dow Chemical Company) dissolved in methanol and diluted to 0.2% in

a 0.25% solution of nonionic surfactant in water. The ¹⁴C herbicide spot treatment was localized to the adaxial surface of the leaf, midway between the leaf tip and the leaf base. The treated plants were then returned to the growth chamber.

Sampling

At 2, 4, 8, 24, and 72 h after treatment (HAT), 10 plants from both vernalization treatments were harvested. Half of the plants from each vernalization treatment were previously treated with clopyralid, and half had received the aminopyralid treatment. At harvest, each plant was separated into seven sections: leaves above the treated leaf, leaves below the treated leaf, crown, roots and associated belowground structures, treated section of the treated leaf, tip of the treated leaf, and base of the treated leaf. At harvest, the treated section of the treated leaf was rinsed with a 1:1 solution of MeOH:dH₂O to remove nonabsorbed radioactivity. All sections were dried to a constant weight in an oven for ≥ 3 d before recording sample dry weights. Rinsate samples were analyzed for total radioactivity using a liquid-scintillation spectrometer. Tissue samples were processed using a biological oxidizer to recover absorbed ¹⁴C material as ¹⁴CO₂, followed by quantification via liquid-scintillation spectrometry.

Experimental Design and Statistical Analysis

The experiment was conducted as a split-split-plot design, with vernalization treatment as the main plot, herbicide treatment as the subplot, and plant section as the sub-subplot. Each treatment combination was replicated for 5 plants per trial, with the trial replicated twice in late fall of 2015 and 2016.

Percent recovery of applied material was calculated by summing the total amount of radioactive material recovered from an entire plant adjusted for oxidizer and liquid-scintillation spectrometry instrument efficiency (both >95% on average). Absorption was calculated as the total radioactivity within the plant as a percentage of the total radioactivity applied. Translocation was calculated as the total radioactivity within a plant section as a percentage of the total radioactivity applied. The entire leaf to which the herbicide was applied is referred to as the “site of application” from which herbicide transport to the rest of the plant occurs. For translocation to the belowground tissue, the roots and associated belowground perennial survival structures section was used. For translocation to the aboveground tissue, all aboveground tissue except the treated leaf was used. For translocation to the entire plant, all plant tissue except the treated leaf was used. ANOVA was conducted using SAS (SAS Institute, 100 SAS Campus Drive, Cary, NC 27513) PROC MIXED, with fixed effects of vernalization treatment, herbicide treatment, and harvest interval and random effect of plant replicate and trial replicate. Eleven outliers were identified using outlierTest in R, and trials were combined or separated as indicated by lack of significant ANOVA results by trial replicate. Translocation data underwent log transformations in order to conform to homoscedasticity and normality assumptions for ANOVA. Translocation to the roots and belowground structures, translocation to the aboveground plant tissue, absorption, and recovery data were analyzed for main effects and interactions.

Data were regressed in R using the DRC and QPCR packages for the analysis of response curves and model fitting, according to the methods of Kniss et al. (2011), back-transforming if necessary (Lee 1986). The first trial for the absorption data was fit to a type II Weibull three-parameter model, given by the expression:

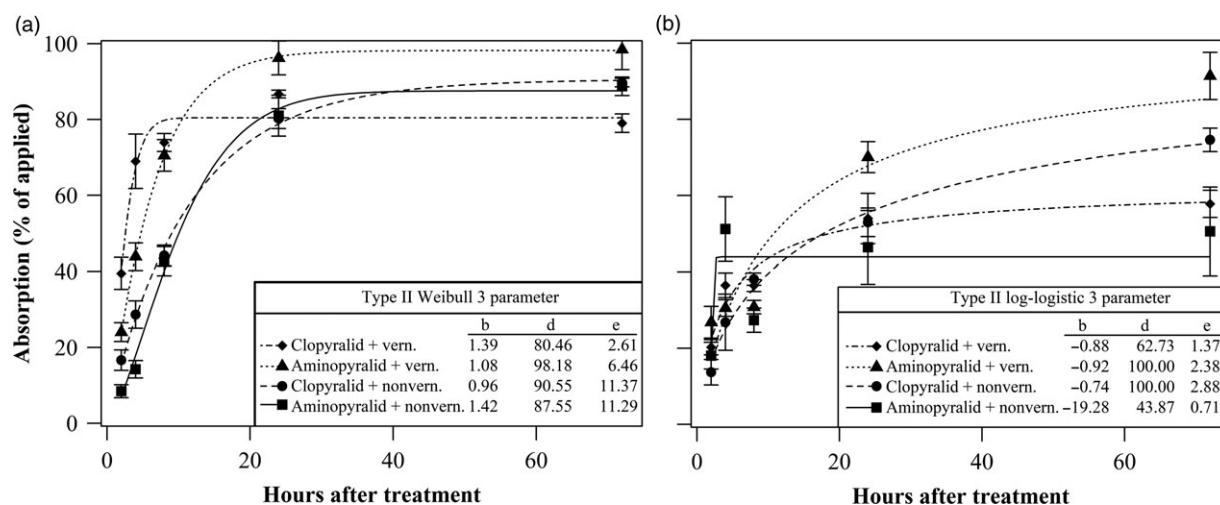


Figure 1. Absorption of ^{14}C , as a percent of applied in the first (A) and second (B) trial, for vernalized and nonvernalized *Chondrilla juncea* plants treated with clopyralid and aminopyralid, harvested at 2, 4, 8, 24, and 72 h after treatment. Vernalization status was significant, while herbicide treatment was not significant ($\alpha = 0.05$) for the first trials. Herbicide treatment was significant, while vernalization status was not significant ($\alpha = 0.05$) for second trial. Error bars indicate standard error of the mean. Data were fit to a type II Weibull three-parameter distribution for the first trial and a type II log-logistic three-parameter distribution for the second trial, indicated by accompanying curves, with parameter estimations indicated in the table inset.

$$f(x) = (d)(1 - \exp\{-\exp[b(\log(x) - \log(e))]\}) \quad [1]$$

where b reflects the slope of the curve, corresponding to the rate of absorption, d is the curve's upper limit, and e represents the inflection point of the curve, corresponding to 50% of total absorption (t_{50}). The second trial for the absorption data, as well as translocation to aboveground tissue data, to belowground tissue data, and to the entire plant data, was fit to type II log-logistic three-parameter models, given by the expression:

$$f(x) = \frac{d}{\{1 + \exp(b[\log(x) - e])\}} \quad [2]$$

where b reflects the slope of the curve, corresponding to the rate of absorption or translocation, d is the curve's upper limit, and $\log(e)$ represents the inflection point of the curve, corresponding to 50% of total absorption or translocation (t_{50}). The best-fit model for each data type and trial was determined via Akaike information criterion and Akaike weight evidence ratios, with parameter comparisons conducted using the DRC package in R.

Results and Discussion

Absorption

Percent recovery of ^{14}C averaged above 95%, and did not differ by harvest interval. Absorption data were analyzed by trial due to a significant trial effect ($P \leq 0.0001$). Absorption into the leaf was similar for aminopyralid and clopyralid treatments in both trials. For the first trial, absorption of ^{14}C by *C. juncea* plants differed by vernalization status ($P \leq 0.0001$) and increased over time ($P \leq 0.0001$), and for both vernalization treatments absorption had reached maximum before 72 HAT (Figure 1A). Model fit indicated that although more ^{14}C was absorbed by vernalized plants at the earlier harvest intervals ($P \leq 0.0001$, $t_{50v} = 4.46$ HAT, $t_{50nv} = 11.53$ HAT), maximum absorption was similar between vernalization treatments ($P = 0.8774$), with estimated absorption maximums of 90.7% and 89.3% of total applied ^{14}C for vernalized and nonvernalized plants, respectively (Figure 1A).

For the second trial, absorption was similar between herbicide treatments over time and vernalization treatments over time, although some clear trends for herbicide and vernalization treatments did occur. At 72 HAT, a clear separation between vernalization treatments occurred for both aminopyralid and clopyralid. Additionally, model fit illustrated more ^{14}C aminopyralid was absorbed by vernalized plants compared with nonvernalized plants at the earlier harvest intervals, maximum ^{14}C aminopyralid absorption was greater for vernalized plants, and for nonvernalized plants, more ^{14}C clopyralid was absorbed at the earlier harvest intervals (Figure 1B). Interestingly, at 72 HAT, vernalized plants absorbed more aminopyralid but less clopyralid than nonvernalized plants. This trend also appears in the first trial, but separation between the treatments is not as clear. As in the first trial, more herbicide was absorbed over time ($P \leq 0.0001$), but absorption increases more slowly over time than in the first trial (Figure 1A and B). Overall, the same trends occur for both trials, with vernalized plants absorbing more aminopyralid but less clopyralid than nonvernalized plants by 72 HAT. Differences between the two trial years may be attributed to annual precipitation and fall temperature differences between 2015 and 2016, when the *C. juncea* root sections were harvested. In 2015 the field site received 19.91 cm of annual precipitation, while in 2016 it received 35.69 cm of annual precipitation; additionally, fall temperatures remained above 4 C until November of 2016, while in 2015 temperatures below 4 C occurred as early as October (AgWeatherNet 2020).

The faster rate of initial absorption in the vernalized plants from the first trial is relevant for the timing of herbicide field applications. Increased absorption after vernalization may be indicative of increased aboveground growth in the spring. By 72 HAT, both vernalized and nonvernalized plants absorbed a similar percentage of the total radioactive herbicide applied, the increased rate of absorption by vernalized plants immediately after application may have been due to a more rapid onset of herbicide symptomology in targeted *C. juncea* plants and the resulting breakdown of transport, likely reducing translocation to the belowground sinks. Absorption of clopyralid by *C. juncea*, both in terms of pattern (biphasic) and total quantity (~80%), was similar to absorption

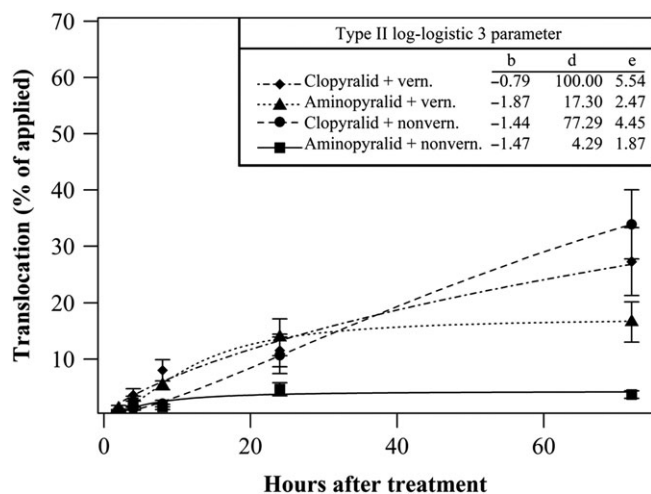


Figure 2. Translocation of [¹⁴C]aminopyralid and [¹⁴C]clopyralid to entire *Chondrilla juncea* plants, as a percent of applied, for vernalized and nonvernalized plants harvested at 2, 4, 8, 24, and 72 h after treatment. Error bars indicate standard error of the mean. Data were fit to a type II log-logistic three-parameter distribution, indicated by accompanying curves, and with parameter estimations indicated in the table inset.

observed in *C. arvensis* (Bukun et al. 2009). Interestingly, absorption of aminopyralid by *C. juncea* (also ~80%) (Bukun et al. 2009) was greater than that observed for *C. arvensis* (~60%). A similar absorption pattern was also observed for aminocyclopyrachlor in *C. juncea* (Bell et al. 2011).

Translocation

Translocation to the entire plant and translocation to aboveground and belowground tissue all had no main effect for trial, and each was averaged over trials. Both herbicide treatment and vernalization treatment had an impact on total translocation to the entire plant, evidenced by t_{50} and maximum absorption comparisons using the e and d parameters (Figure 2). Maximum absorption was different between aminopyralid vernalization treatments ($P = 0.002$), with estimated absorption maximums of 17.30% and 4.29% of total applied ¹⁴C for vernalized and nonvernalized plants, respectively. For the clopyralid treatment, maximum absorption was similar between vernalization treatments, while the t_{50} for the vernalized plants ($t_{50v} = 5.54$) was significantly more than for nonvernalized plants ($t_{50nv} = 4.45$, $P = 0.0338$). For the aminopyralid treatment, the vernalized plants again had a higher t_{50} value compared with the nonvernalized plants, but the difference was smaller and not significant. There was also a difference between the herbicide treatments, such that plants treated with clopyralid exhibited higher t_{50} values compared with aminopyralid-treated plants. The difference was only significant for the vernalized plants ($P = 0.0006$).

The general trend of increased translocation to the roots and belowground perennial survival structures over time was significantly different according to the vernalization treatment but not the herbicide treatment (Figure 3). A much greater amount of ¹⁴C material was translocated to aboveground tissue compared with belowground tissue (Figure 4). No greater than 6%, on average, of the total applied ¹⁴C material was detected in the belowground tissue at any harvest interval, while as much as 30%, on average, was detected in the aboveground tissue. Over time, translocation to both above- and belowground tissue increased ($P_{\text{aboveground}} \leq 0.0001$, $P_{\text{belowground}} \leq 0.0001$). The scale of the

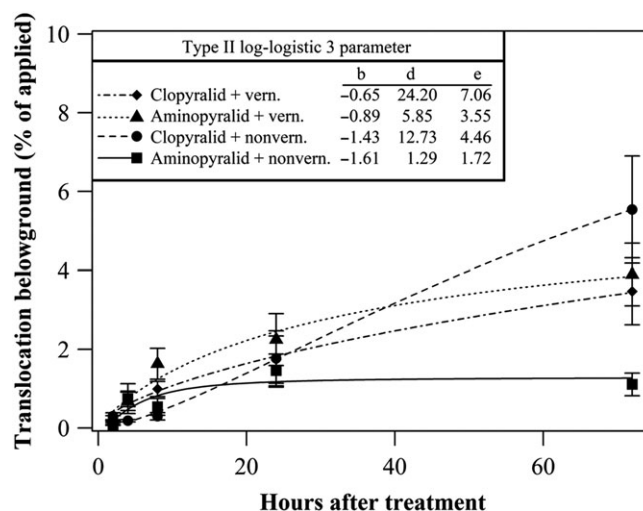


Figure 3. Translocation of [¹⁴C]aminopyralid and [¹⁴C]clopyralid to belowground tissue of *Chondrilla juncea*, as a percent of applied, for plants harvested at 2, 4, 8, 24, and 72 h after treatment. Vernalization status was significant, while herbicide treatment was not significant ($\alpha = 0.05$). Error bars indicate standard error of the mean. Data were fit to a type II log-logistic three-parameter distribution, indicated by accompanying curves, and with parameter estimations indicated in the table inset.

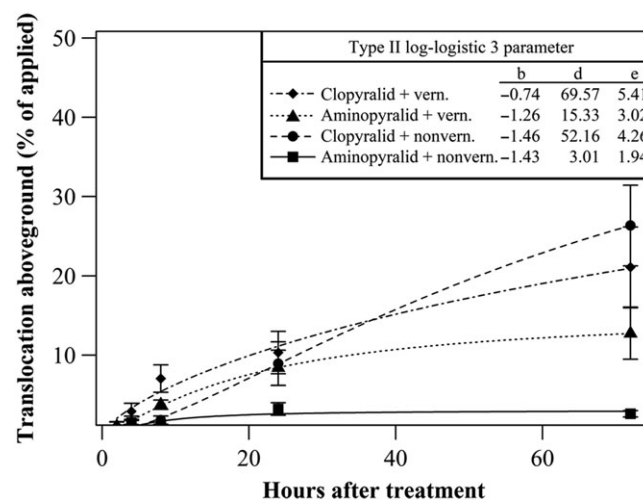


Figure 4. Translocation of [¹⁴C]clopyralid and [¹⁴C]aminopyralid to aboveground tissue of *Chondrilla juncea*, as a percent of applied, for vernalized and nonvernalized plants harvested at 2, 4, 8, 24, and 72 h after treatment. Error bars indicate standard error of the mean. Data were fit to a type II log-logistic three-parameter distribution, indicated by accompanying models, and with parameter estimations indicated in the table inset.

increase was dependent on vernalization treatment for belowground translocation ($P_{\text{vernalization}} \leq 0.0001$), while aboveground translocation was dependent on both vernalization treatment ($P_{\text{vernalization}} \leq 0.0001$) and herbicide treatment ($P_{\text{herbicide}} = 0.0001$).

Translocation to belowground tissue was similar from 2 to 72 HAT for vernalized plants, while for nonvernalized plants more clopyralid than aminopyralid had been translocated belowground by 72 HAT. Translocation to aboveground tissue was more similar between vernalized and nonvernalized plants than translocation to belowground tissue. For translocation to aboveground tissue, there were greater differences between herbicide treatments than for translocation to belowground tissue. A similar trend is present

for both vernalization treatments, with vernalized plants translocating more ^{14}C material to aboveground tissue at the earlier harvest intervals. The trend persists to 72 HAT for the aminopyralid treatment. There was also more ^{14}C material translocated to the aboveground tissue for plants treated with clopyralid compared with plants treated with aminopyralid. Despite the presence of such data trends, the t_{50} values for aboveground translocation were similar.

The translocation of pyridine herbicides, such as clopyralid and aminopyralid, has been investigated in other weed species (Bell et al. 2011; Bukun et al. 2009, 2010; Dos Reis et al. 2015; Hall and Vanderborn 1988; Orfanedes et al. 1993; Turnbull and Stephenson 1985; Valenzuela-Valenzuela et al. 2001; Zollinger et al. 1992). For aminocyclopyrachlor, translocation above and belowground has been reported to be species dependent (Bell et al. 2011; Bukun et al. 2010; Dos Reis et al. 2015). Prickly lettuce (*Lactuca serriola* L.) was reported to have translocated a low proportion of the aminocyclopyrachlor applied (<3%), likely due to hypersusceptibility of this species to aminocyclopyrachlor. The small amount of translocation of aminocyclopyrachlor that does occur in *L. serriola* is predominantly aboveground (<2%), as is the case for trumpetflower [*Tecoma stans* (L.) Juss. ex Kunth] (<5% total translocation and <4% aboveground translocation) (Bell et al. 2011; Dos Reis et al. 2015).

Yellow starthistle (*Centaurea solstitialis* L.) and *C. arvensis* were reported to translocate <20% and <40%, respectively, of applied aminocyclopyrachlor, with more translocation aboveground compared with belowground (<15% and <30%, respectively) (Bell et al. 2011; Bukun et al. 2010). The same trend was also observed in *C. solstitialis* and *C. arvensis* for clopyralid translocation (Bell et al. 2011; Bukun et al. 2009, 2010; Valenzuela-Valenzuela et al. 2001). Perennial sow thistle (*Sonchus arvensis* L.) and hemp dogbane (*Apocynum cannabinum* L.) followed the same pattern for clopyralid translocation and fluoxypyr translocation (Orfanedes et al. 1993; Zollinger et al. 1992). Sunflower (*Helianthus annuus* L.) and rapeseed (*Brassica napus* L.) also translocated more clopyralid and picloram to aboveground structures compared with belowground structures (Hall and Vanderborn 1988).

Chondrilla juncea breaks with this translocation pattern, translocating less aminocyclopyrachlor than *C. solstitialis* and more belowground than aboveground, possibly due to lower sensitivity to aminocyclopyrachlor (Bell et al. 2011). Another deviation from the general trend of more translocation to aboveground tissues occurs in other studies with *C. arvensis*. Translocation of clopyralid and aminopyralid in *C. arvensis* has also been observed to be similar between the aboveground and belowground tissue, with higher amounts of clopyralid translocation compared with aminopyralid (Bukun et al. 2009; Turnbull and Stephenson 1985). The discrepancy in clopyralid translocation could be due to the lack of overspray and low dosage applied by Turnbull and Stephenson (1985), which could have led to a sublethal plant response, resulting in more material translocating belowground. The low amount of aminopyralid translocation in *C. arvensis*, which occurred at similar rates in above- and belowground tissue, was attributed to the high biological activity of aminocyclopyrachlor (Bukun et al. 2009). Overall, translocation was affected both by the specific pyridine herbicides and the plant species examined in these studies (Bell et al. 2011; Bukun et al. 2009, 2010; Dos Reis et al. 2015; Orfanedes et al. 1993; Turnbull and Stephenson 1985; Valenzuela-Valenzuela et al. 2001; Zollinger et al. 1992). Additionally, in the majority of observations of susceptible species, more aboveground- than belowground-directed translocation has

been reported, similar to what is observed in *C. juncea* treated with clopyralid and aminopyralid in the present study.

Differences in the source–sink relationships of clopyralid and aminopyralid in vernalized and nonvernalized *C. juncea* may contribute to the differential efficacy observed in the field. This is particularly evident when considering changes in herbicide mobilization to the roots and perennial survival structure sinks, due to the reproductive mode used by *C. juncea*. More ^{14}C material translocates to the aboveground tissue compared with the belowground tissue, which correlates with the known difficulty of targeting the roots and perennial survival structures of *C. juncea*. Vegetative reproduction is a prevalent reproductive mode in *C. juncea*. The roots and belowground perennial survival structures are integral in vegetative reproduction (Bukun et al. 2009). It is evident that more total translocation is occurring in vernalized plants and in plants treated with clopyralid versus aminopyralid. The increased aminopyralid translocation occurring in vernalized plants is consistent with increased belowground mobilization, and thus could indicate improved control with spring application timings. However, when coupled with the low mobilization to the belowground structures, this may not be meaningful from a management standpoint.

Vernalization is a critical process affecting absorption and translocation in perennial plants. Herbicide applications will likely be more effective if the process of vernalization and how it changes source–sink relationships within *C. juncea* were better understood. The present study illustrates *C. juncea*'s differential response to the two related herbicides, clopyralid and aminopyralid, before and after vernalization. Plants treated with aminopyralid exhibit much less total and aboveground translocation before vernalization. Plants treated with aminopyralid also exhibited less total and aboveground translocation than clopyralid-treated plants. Vernalized plants translocated more herbicide, absorbed more material in the treated leaf, and translocated material to the belowground tissue more rapidly than nonvernalized plants. The increase in herbicide mobilization postvernalization is consistent with the increase in photoassimilate mobilization known to occur in other perennial asters after vernalization (Tworkoski 1992; Wilson et al. 2006). In field experiments, a much lower dose of aminopyralid than clopyralid is required for similar levels of control, 10 and 210 g ae ha⁻¹, respectively, for both spring and fall applications (Spring et al. 2018). The breakdown in photoassimilate transport associated with such control could be responsible for the decrease in aminopyralid translocation compared with clopyralid translocation. More research is needed to determine how to optimize timing of aminopyralid and clopyralid applications in the field based on vernalization status and to understand how soil active residues might affect the outcome of aminopyralid and clopyralid herbicide applications for *C. juncea* management.

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