Weed Science 2017 65:588–602

Temperature Influences Efficacy, Absorption, and Translocation of 2,4-D or Glyphosate in Glyphosate-Resistant and Glyphosate-Susceptible Common Ragweed (*Ambrosia artemisiifolia*) and Giant Ragweed (*Ambrosia trifida*)

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Glyphosate and 2,4-D have been commonly used for control of common and giant ragweed before planting of corn and soybean in the midwestern United States. Because these herbicides are primarily applied in early spring, environmental factors such as temperature may influence their efficacy. The objectives of this study were to (1) evaluate the influence of temperature on the efficacy of 2,4-D or glyphosate for common and giant ragweed control and the level of glyphosate resistance and (2) determine the underlying physiological mechanisms (absorption and translocation). Glyphosate-susceptible (GS) and glyphosate-resistant (GR) common and giant ragweed biotypes from Nebraska were used for glyphosate dose–response studies, and GR biotypes were used for 2,4-D dose–response studies conducted at two temperatures (day/night [d/n]; low temperature [LT]: 20/11 C d/n; high temperature [HT]: 29/17 C d/n). Results indicate improved efficacy of 2,4-D or glyphosate at HT compared with LT for common and giant ragweed control regardless of susceptibility or resistance to glyphosate. The level of glyphosate resistance decreased in both the species at HT compared with LT, primarily due to more translocation at HT. More translocation of 2,4-D in GR common and giant ragweed at HT compared with LT at 96 h after treatment could be the reason for improved efficacy. Similarly, higher translocation in common ragweed and increased absorption and translocation in giant ragweed resulted in greater efficacy of glyphosate at HT compared with LT. It is concluded that the efficacy of 2,4-D or glyphosate for common and giant ragweed control can be improved if applied at warm temperatures (29/17 C d/n) due to increased absorption and/or translocation compared with applications during cooler temperatures (20/11 C d/n).

Nomenclature: 2,4-D, glyphosate; common ragweed, *Ambrosia artemisiifolia* L.; giant ragweed, *Ambrosia trifida* L.; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.

Key words: Herbicide efficacy, higher translocation, increased absorption, warm temperature.

Common ragweed and giant ragweed are important broadleaf annual weeds of the Asteraceae family native to the United States (Abul-Fatih and Bazzaz 1979; Bassett and Crompton 1975). They are widely distributed in diverse agroecosystems, including roadsides, low-fertility areas, field edges, and agronomic fields (Johnson et al. 2006; Jordan et al. 2007). Early spring emergence is a typical characteristic of common ragweed (Barnes et al. 2017) and giant ragweed (Kaur et al. 2016) in Nebraska; therefore, preplant control with herbicides is the most effective method for the management of early-season ragweed infestations (Jhala et al. 2014; Johnson et al. 2006; Jordan et al. 2007). Nevertheless, follow-up PRE and/or POST herbicides are required for effective season-long control of both ragweed species in corn and soybean (Ganie et al. 2016, 2017; Jhala et al. 2014). Glyphosate has been the most commonly used herbicide for preplant or POST control of ragweed species in glyphosate-resistant (GR) corn or soybean in the Midwest; however, the evolution of ragweed species resistant to glyphosate and/or acetolactate synthase inhibitors has reduced the number of available herbicide options (Chandi et al. 2012; Patzoldt and Tranel 2002; Patzoldt et al. 2001; Regnier et al. 2016).

Growth regulator herbicides such as 2,4-D are effective for preplant control of both common and giant ragweed (Ganie et al. 2016; Johnson et al. 2006; Jordan et al. 2007). Previously, Ganie et al. (2016) and Jhala et al. (2014) reported ≥87% control of GR giant ragweed at 14 d after treatment (DAT) with a preplant burndown application of 2,4-D amine. Similarly, 2,4-D choline plus glyphosate resulted in >93% control of GR common ragweed at 21 DAT in a greenhouse study (Ganie et al. 2017). However, the continuous evolution of herbicide-resistant weeds,

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DOI: 10.1017/wsc.2017.32

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particularly those resistant to multiple herbicide sites of action, are limiting the number of effective herbicide options (Tranel et al. 2011). In addition, in the absence of an herbicide with a novel site of action being developed for over three decades (Duke 2012), it is vital to attain the best possible results with available herbicides by applying them at the optimal weed growth stage and under appropriate environmental conditions (Godar et al. 2015). Herbicide efficacy is affected by plant characteristics, including plant type and/or growth stage (Chahal et al. 2015), along with environmental factors such as light intensity, temperature, water stress, relative humidity, nutrient status, and atmospheric pollution (Anderson et al. 1993; Cole 1983; Gerber et al. 1983; Godar et al. 2015; Hull 1970; Johnson and Young 2002; Price 1983). Previous studies have reported that growth temperature before, during, or after herbicide application has a major influence on herbicide efficacy: for example, control of johnsongrass [*Sorghum halepense* (L.) Pers.] with glyphosate was greater when applied at 35 C compared with 24 C (McWhorter et al. 1980). Similarly, the efficacy of glyphosate for control of bermudagrass [*Cynodon dactylon* (L.) Pers.] improved at 32 C compared with 22 C at 40% relative humidity (Jordan 1977). In contrast, mesotrione showed higher efficacy for control of common waterhemp (*Amaranthus rudis* Sauer) and large crabgrass [*Digitaria sanguinalis* (L.) Scop.] at 18 C compared with 32 C (Johnson and Young 2002). Similarly, Palmer amaranth (*Amaranthus palmeri* S. Wats.) was more sensitive to mesotrione at low (25/15 C d/n) compared with high temperatures (40/30 C d/n) (Godar et al. 2015). Increased absorption or translocation at higher temperatures usually results in improved herbicide efficacy (Pline et al. 1999), whereas improved efficacy at lower temperatures might be due to a more slowly metabolized herbicide (Godar et al. 2015).

The level of glyphosate resistance may vary with the temperature at which the GR weed species is growing. For example, hairy fleabane [*Conyza bonariensis* (L.) Cronq.] showed 2- to 10-fold greater resistance to glyphosate at high-temperature (HT) regimes (28/22 or 34/28 C d/n) compared with low-temperature (LT) regimes (16/10 or 22/16 C d/n) (Kleinman et al. 2011). Similarly, the level of glyphosate resistance in johnsongrass and rigid ryegrass (*Lolium rigidum* Gaudin) varied with the temperature, and these species were relatively more susceptible (50% to 70%) to the labeled rate of glyphosate at 19 and 8 C compared with <50% or 40% control at 30 and 19 C, respectively (Vila-Aiub et al. 2013). The higher level of glyphosate resistance in barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] at 30 C compared with 20 C was due to a 2-fold increase in glyphosate uptake at 20 C in both GR and glyphosate-susceptible (GS) biotypes (Nguyen et al. 2015).

Preplant burndown herbicides such as glyphosate and/or 2,4-D are applied early in the spring, typically from March 15 to May 10 in Nebraska and several other states in the midwestern United States for control of winter annual weeds such as henbit (*Lamium amplexicaule* L.), field pennycress (*Thlaspi arvense* L.), and horseweed [*Conyza canadensis* (L.) Cronq.] and early-emerging summer weeds such as common and giant ragweed (Jhala 2016). The daily temperature during early spring is highly variable in Nebraska, which can affect weed growth and development (Leon et al. 2004; Schwabe 1957) and the efficacy of preplant burndown herbicides (Hammerton 1967).

Scientific literature is not available on the effect of varying temperatures on the efficacy of 2,4-D or glyphosate for control of common and giant ragweed or on the level of glyphosate resistance. The objectives of this study were to (1) evaluate the influence of temperature on the efficacy of 2,4-D or glyphosate for common and giant ragweed control and the level of glyphosate resistance and (2) determine the underlying physiological mechanisms (absorption and translocation). We hypothesized that higher temperatures would improve the efficacy of 2,4-D or glyphosate in common and giant ragweed due to increased absorption and/or translocation, and that temperature would affect the level of glyphosate resistance.

Materials and Methods

Plant Material and Growth Conditions. The GR common ragweed biotype was collected from a grower's field in Gage County, NE (40.44°N, 96.62°W). The GR giant ragweed biotype was collected from a grower's field in Butler County, NE (41.25°N, 97.13°W). The level of resistance in the common and giant ragweed biotypes were 19- and 14-fold, respectively, compared with the known GS biotypes (Ganie and Jhala 2017; Rana et al. 2013). GS biotypes of common and giant ragweed were collected from the South Central Agricultural Laboratory, University of Nebraska–Lincoln, Clay Center, NE (40.52°N, 98.05°W), and were used in this study for comparison. The seeds were cleaned and stored at 4 C until used in this study. Giant ragweed is characterized by high seed dormancy at maturity and relatively low germination rates (Page and Nurse 2015), but dormancy can be broken by the cold stratification of seeds. Therefore, to break seed dormancy, seeds were packed in mesh bags and stratified by placing them between layers of a mixture of potting mix and soil (3:1) in plastic boxes (58 by 42 by 15 cm), which were then kept in a freezer for 3.5 mo (Kaur et al. 2016). GR and GS common and giant ragweed seeds were germinated in plastic trays (25 by 15 by 5 cm) filled with commercial potting mix (Berger BM1 All-Purpose Mix, Berger Peat Moss, Saint-Modeste, QC, Canada), and uniform-sized individual seedlings were transplanted at the 2-leaf stage into square plastic pots (6 by 6 by 6.5 cm) containing a 3:1 mixture of potting mix to soil. Plants were supplied with water daily and fertilized once a week after transplanting. Growth conditions in the greenhouse were maintained at 26/21 C d/n temperature, 65 ± 5% relative humidity, and a 15-h photoperiod supplemented with sodium vapor lamps providing 120 μmol m^{-2} s^{-1} photon flux. Four or five days after transplanting, healthy uniform-sized plants (5- to 6-cm tall) were transferred to growth chambers maintained at two temperature regimes: LT (20/11 C d/n) and HT (29/17 C d/n). The transition of temperatures between day and night or vice versa were programmed to begin progressively over a 2-h period to reach the set value without causing abrupt temperature shock to the plants. Plants were maintained at a 15/9 h d/n length, and the light sources in the growth chambers were incandescent and fluorescent bulbs delivering 550 μmol m^{-2} s^{-1} photon flux at the plant canopy level. Growth chambers were maintained at 70 ± 5% relative humidity throughout the experiment, and the plants were watered regularly.

Dose–Response Experiments. GR and GS biotypes of both common ragweed and giant ragweed (grown under the conditions described earlier) were treated with different rates of glyphosate (Touchdown HiTech®, Syngenta Crop Protection, P.O. Box 18300, Greensboro, NC 27419-8300) when the plants were 10- to 12-cm tall (8- to 10-leaf stage). GR biotypes of common or giant ragweed were used in a dose–response study with 2,4-D amine (Winfield Solutions, LLC, St Paul, MN 55164). For each study, glyphosate or 2,4-D was applied at rates of 0, 0.06×, 0.12×, 0.25×, 0.5×, 1×, 2×, and 4×, where "×" is 560 g ae ha^{-1} for 2,4-D or 1,260 g ae ha^{-1} for glyphosate. An additional 8 × rate of glyphosate was used for the GR biotypes. Herbicide treatments were prepared in distilled water and nonionic surfactant (Induce®, Helena Chemical, Collierville, TN) was added to both 2,4-D, and glyphosate at 0.25% v/v. Ammonium sulfate (DSM Chemicals North America, Augusta, GA) was added to glyphosate treatments at 1% w/v. The herbicide treatments were applied with an automated bench-type sprayer (Research Track Sprayer, De Vries Manufacturing, RR 1 Box 184, Hollandale, MN) equipped with a flat-fan nozzle tip (80015LP TeeJet® tip, Spraying Systems, Wheaton, IL) delivering 187 L ha^{-1} at 207 kPa in a single pass at 4.8 km h^{-1}. The temperature, relative humidity, and light intensity at the time of herbicide application were 26 C, 65%, and 15 μmol m^{-2} s^{-1}, respectively. Plants were returned to their respective growth chambers within 30 min after herbicide treatment. The experiments were arranged in a factorial randomized complete block design (RCBD) with a combination of two temperature regimes (LT and HT) and eight (or nine) herbicide rates. The treatments were replicated four times, and the experiment was repeated twice with the same procedure, except that the growth chambers were switched.

Visual assessments of control were recorded at 21 DAT using a 0% to 100% scale, with 0% equivalent to no control and 100% equivalent to complete control or mortality of the plants. Percent control estimates for treated plants were assessed based on a comparison with nontreated control plants with respect to symptoms such as twisting/epinasty (2,4-D) or chlorosis, necrosis, stand loss, and stunting (glyphosate). Aboveground biomass of each plant was cut close to the base at 21 DAT, oven-dried at 65 C for 3 d, and weighed (g). The biomass data were converted into percent biomass reduction compared with the nontreated control (Sarangi and Jhala 2017) as:

$$\text{Biomass reduction }(\%) = \left[\frac{(C-B)}{C}\right] \times 100 \qquad [1]$$

where C is the biomass of nontreated control replicates and B is the biomass of an individual treated experimental unit.

Data were subjected to ANOVA in SAS to test the treatment by experiment interactions. Control estimates and biomass reduction data were regressed over herbicide treatments using a four-parameter log-logistic model in the 'drc' package (drc 1.2, Christian Ritz and Jens Strebig, R2.5, Kurt Hornik, online) of R (R Statistical Software, R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org) (Ritz and Streibig 2005):

$$Y = L + \frac{U-L}{1+\exp[S(\log X - \log E)]} \qquad [2]$$

where Y is the response variable (percent control estimates or percent reduction in biomass), L is the lower limit, U is the upper limit, S is the slope of the curve, E is the dose resulting in 50% or 90% control (known as ED_{50} or ED_{90}), and X is the herbicide rate. This model was used to determine ED_{50} or ED_{90} and GR_{50} or GR_{90} (effective doses required for 50% or 90% biomass reduction) from the visual assessment of injury and biomass reduction data, respectively. The level of glyphosate resistance was determined by dividing the ED_{90} and GR_{90} values with the recommended field rate of 1,260 g ae ha^{-1}. Additionally, the ratio of the effective doses (ED_{50}, ED_{90}, GR_{50}, and GR_{90}) of the GR to the GS biotype (R/S ratio) were also determined (Tables 1 and 2), but due to the greater sensitivity of the susceptible biotypes at HT, the comparison may not serve as a stable measure of resistance level across temperature regimes.

Model Goodness of Fit. Root mean square error (RMSE) and modeling efficiency coefficients (EF) were used to determine the goodness of fit for the four-parameter log-logistic model used to analyze the dose–response data (Mayer and Butler 1993):

$$\mathrm{RMSE} = \left[\frac{1}{n}\sum\nolimits_{i=1}^{n}(P_i - O_i)^2\right]^{1/2} \qquad [3]$$

$$\mathrm{EF} = 1 - \left[\sum\nolimits_{i=1}^{n}(O_i - P_i)^2 \Big/ \sum\nolimits_{i=1}^{n}\left(O_i - \overline{O}_i\right)^2\right] \qquad [4]$$

where P_i is the predicted value, O_i is the observed value, $\overline{O}_i$ is the mean observed value, and n is the total number of observations. Smaller RMSE values indicate a superior fit, and EF values closer to 1 indicate more precise predictions.

Absorption and Translocation Experiments. Uniform-sized common and giant ragweed seedlings grown in the greenhouse (as described earlier) were shifted to growth chambers maintained at LT or HT and allowed to acclimatize for 6 to 10 d. Plants 8- to 10-cm tall were treated with ten 1-μl droplets of uniformly labeled [^{14}C]glyphosate (3.3 kBq with specific activity of 1.85 MBq mmol^{-1} [PerkinElmer, 549 Albany Street, Boston, MA]) or uniformly ring labeled [^{14}C]2,4-D (3.3 kBq with specific activity of 5.5 MBq mmol^{-1} [Dow AgroScience 9330 Zionsville Road, Building 306-D2, Indianapolis, IN]) on the upper surface of the fully expanded fourth-youngest leaf. Commercial glyphosate or 2,4-D was added to the respective radioactive solutions to obtain the recommended 1× concentration equivalent to 1,260 g ae ha^{-1} of glyphosate or 560 g ae ha^{-1} of 2,4-D. The plants were returned to the growth chambers within 30 min of treatment. Subsequently, plants were dissected at 24, 48, 72, and 96 h after treatment (HAT) into treated leaf, tissues above treated leaf, and tissues below treated leaf. Treated leaves were rinsed twice in a 20-ml scintillation vial containing 5 ml of wash solution (1:1 v/v mixture of methanol and deionized water and 0.45% Tween-20) for 1 min to remove the unabsorbed herbicide from the surface of the treated leaf. The leaf rinse was mixed with 15 ml of scintillation cocktail (Ecolite-(R), MP Biomedicals, LLC. Santa Ana, CA), and radioactivity was determined by using liquid scintillation spectrometry (LSS) (Tricarb 2100 TR Liquid Scintillation Analyzer, Packard Instrument, Meriden, CT). Plant sections were dried at 55 C for 72 h, combusted in a biological oxidizer (OX-501, RJ Harvey Instrument, Tappan, NY) for 3 min to recover ^{14}C-labeled glyphosate or 2,4-D in a proprietary ^{14}C-trapping scintillation cocktail, and radioassayed using LSS. The chemical nature of ^{14}C-labeled compounds recovered after burning the samples was not determined, but more likely included parent compound in the case of [^{14}C]glyphosate and either parent compound or derivatives or both in the case of [^{14}C]2,4-D. Herbicide absorption and translocation were calculated as (Godar et al. 2015):

$$\%\ \text{Absorption} = \frac{\left[\begin{array}{l}\text{Total radioactivity applied}-\\ \quad\text{radioactvity recovered in wash solution}\end{array}\right]}{\text{Total radioactivity applied}} \times 100 \qquad [5]$$

$$\%\ \text{Translocation} = 100 - \%\ \text{radioactivity in treated leaf} \qquad [6]$$

where % Radioactivity in treated leaf

$$= \frac{\text{Radioactivity recovered in treated leaf}}{\text{Radioactivity absorbed}} \times 100.$$

The experiments were arranged in a factorial treatment combination with two temperatures and four harvest time points. Within each temperature regime, the experimental units were arranged in an RCBD by blocking to overcome variability due to plant size with four replications, and the experiment was repeated twice following the same procedure, except that the growth chambers were switched. Data from the absorption and translocation experiments were subjected to ANOVA in SAS v. 9.3 (SAS Institute, Cary, NC) using the PROC GLIMMIX procedure to test the treatment by experiment interaction. The absorption or translocation data were regressed over harvest time using a best-fit linear model in GraphPad Prism 6 (GraphPad Software, Avenida de la Playa, La Jolla, CA 92037):

$$y = a + bx \qquad [7]$$

where y is the percentage of the applied [^{14}C] glyphosate absorbed or translocated in the plant, a is the intercept or initial absorption or translocation expressed as the percent applied or absorbed, b is the slope or rate of change of the absorption/translocation over time, and x is the time expressed as HAT. To indicate the fit of linear regression, model R^2 values were included in the figures.

The treatment by experiment interactions in the dose–response or the absorption and translocation studies were not significant ($P > 0.05$); therefore, data were combined over the experiments.

Results and Discussion

2,4-D Dose–Response. The sensitivity of common and giant ragweed to 2,4-D varied with the temperature (Figure 1). Required 2,4-D doses to achieve 50% (ED_{50}) and 90% (ED_{90}) control of common ragweed were 187 and 3,805 g ae ha^{-1} at LT compared with 61 and 177 g ae ha^{-1} at HT, respectively (Table 1). In contrast, the ED_{50} and ED_{90} for giant ragweed were 71 and 792 g ae ha^{-1} at LT compared with 13 and 49 g ae ha^{-1} at HT, respectively (Table 1), indicating that giant ragweed was more sensitive to 2,4-D than common ragweed. Results of the biomass reduction revealed that GR_{90} was 2.8 and 2.9 times lower in common and giant ragweed, respectively, at HT compared with LT (Table 2), showing that the efficacy of 2,4-D improved when d/n temperatures were increased from 20/11 C to 29/17 C. Similarly, Kelly (1949) reported that kidney beans (*Phaseolus vulgaris* L.) were more sensitive to 2,4-D at 25 C compared with 5 or 15 C, and the biologically effective rates required at HT were lower compared with the rates required at LT. Likewise, the sensitivity of common flax (*Linum usitatissimum* L.) to 2,4-D improved

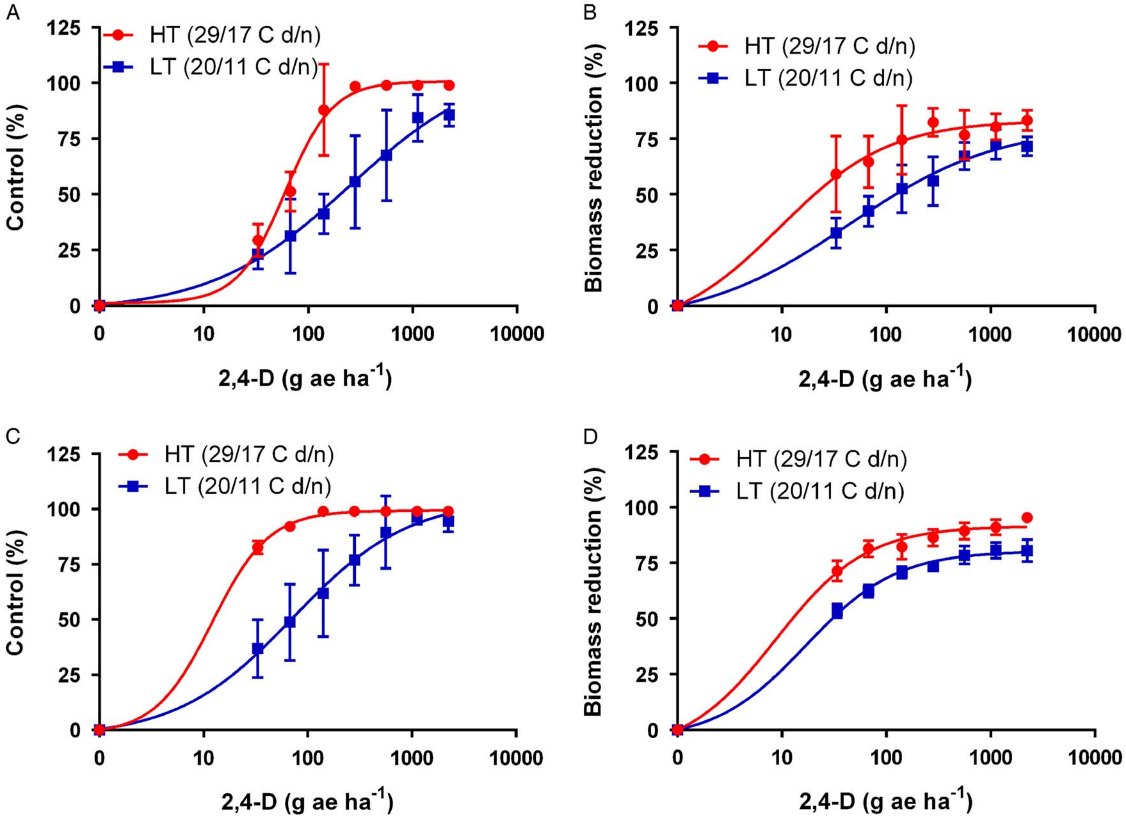

Figure 1. Dose–response curves of common ragweed and giant ragweed to 2,4-D applied at high temperature (HT) and low temperature (LT) regimes at 21 d after treatment: (A) control of common ragweed, (B) biomass reduction of common ragweed, (C) control of giant ragweed, and (D) biomass reduction of giant ragweed.

Table 1. Estimates of regression parameters and 2,4-D or glyphosate doses required for 50% (ED_{50}) and 90% (ED_{90}) control of glyphosate-resistant (GR) and glyphosate-susceptible (GS) common ragweed and giant ragweed at 21 d after treatment in whole-plant dose–response studies conducted at high- and low-temperature regimes in growth chambers.

	Low temperature (d/n 20/11 C)[a]					High temperature (d/n 29/17 C)[a]				
	Regression parameters[b]			Effective herbicide doses		Regression parameters[b]			Effective herbicide doses	
Herbicide	*S*	*L*	*U*	ED_{50} (± SE)	ED_{90} (± SE)	*S*	*L*	*U*	ED_{50} (± SE)	ED_{90} (± SE)
	g ae ha^{-1}					g ae ha^{-1}				
Common ragweed										
2,4-D	0.6 (0.2)	− 2.0 (1.0)	103 (4)	187 (22)	3,805 (166)	1.9 (0.2)	1.2 (0.7)	101 (2)	61 (4)	177 (21)
Glyphosate										
GS biotype	0.8 (0.2)	0.7 (0.4)	102 (6)	437 (50)	6,963 (2,159)	1.5 (0.2)	1.5 (0.8)	101 (3)	130 (11)	587 (96)
GR biotype	0.7 (0.2)	−1.6 (1.0)	73 (13)	2,821 (343)	118,371 (35,427)	1.2 (0.3)	1.8 (1.0)	97 (10)	1,307 (140)	8,354 (2,145)
Resistance level[c]	—	—	—	—	94.0	—	—	—	—	6.6
R/S ratio	—	—	—	6.5	17.0	—	—	—	10.0	14.2
Giant ragweed										
2,4-D	0.8 (0.2)	−3.3 (2.3)	104 (8)	71 (11)	792 (192)	1.6 (0.1)	−1.9(1.0)	99 (0.30)	13 (1)	49 (1.7)
Glyphosate										
GS biotype	1.8 (0.3)	0.3 (0.2)	100 (2.5)	119 (15)	468 (168)	1.7 (0.3)	0.0 (0.0)	99 (1.6)	62 (5)	244 (35)
GR biotype	0.8 (0.5)	4.6 (2.9)	77 (2.4)	1,429 (280)	66,207 (20,918)	1.9 (1.4)	3.5 (2.0)	86 (3.7)	1,164 (144)	5,751 (1,445)
Resistance level[c]	—	—	—	—	52	—	—	—	—	4.6
R/S ratio	—	—	—	12.0	141.5	—	—	—	18.8	23.6

[a] Abbreviations: d/n, day/night temperatures; ED_{50}, effective 2,4-D or glyphosate dose required for 50% control of common or giant ragweed; ED_{90}, effective 2,4-D or glyphosate dose required for 90% control of common or giant ragweed.

[b] Regression parameters *S* (slope), *L* (lower limit), and *U* (upper limit) of the four-parameter log-logistic model $(Y = L + \{U - L/1 + \exp[S(\log X - \log E)]\})$ were determined by using the nonlinear least-square function of the statistical software R.

[c] The resistance level was determined compared with the field rate of glyphosate (i.e., 1,260 g ae ha^{-1}), because the GS biotypes became too sensitive at the high temperature regime, leading to instability in the resistance level determined on the basis of the R/S ratio.

Table 2. Estimates of regression parameters and 2,4-D or glyphosate doses required for 50% (GR_{50}) and 90% (GR_{90}) biomass reduction of glyphosate-resistant (GR) and glyphosate-susceptible (GS) common ragweed and giant ragweed at 21 d after treatment in greenhouse whole-plant dose–response studies conducted at high- and low-temperature regimes.

	Low temperature (d/n 20/11 C)[a]					High temperature (d/n 29/17 C)[a]				
	Regression parameters[b]			Effective herbicide doses		Regression parameters[b]			Effective herbicide doses	
Herbicide	S	L	U	GR_{50} (± SE)	GR_{90} (± SE)	S	L	U	GR_{50} (± SE)	GR_{90} (± SE)
	g ae ha^{-1}					g ae ha^{-1}				
Common ragweed										
2,4-D	0.6 (0.2)	−0.9 (0.3)	81 (7)	20 (8)	365 (85)	0.8 (0.4)	−0.7 (0.1)	87 (4)	17 (7)	128 (59)
Glyphosate										
GS biotype	0.7 (0.3)	−0.5 (3.0)	87 (7)	45 (17)	1,249 (246)	1.3 (0.4)	−0.7 (0.5)	97 (2)	39 (9)	210 (62)
GR biotype	0.6 (0.3)	0.0 (0.0)	79 (5)	323 (75)	3,869 (676)	1.1 (0.2)	−1.9 (1.5)	93 (12)	306 (61)	2,022 (108)
Resistance level	—	—	—	—	3.0	—	—	—	—	1.6
R/S ratio	—	—	—	7.2	3.1	—			7.8	9.6
Giant ragweed										
2,4-D	1.0 (0.7)	−0.6 (0.1)	80 (1)	15 (2)	277 (81)	1.4 (0.9)	−0.4 (0.2)	92	25 (5)	94 (42)
Glyphosate										
GS biotype	1.1 (0.1)	−0.6 (0.4)	87 (1)	59 (12)	956 (113)	1.5 (0.2)	−0.1 (0.0)	93 (2)	49 (16)	154 (67)
GR biotype	1.1 (0.2)	−1.0 (0.6)	79 (3)	349 (71)	5,879 (1,945)	1.2 (0.3)	−0.7 (0.5)	88 (2)	218 (44)	2,293 (621)
Resistance level	—	—	—	—	4.7	—	—	—	—	1.8
R/S ratio	—	—	—	5.9	6.1	—	—	—	4.4	14.9

[a] Abbreviations: d/n, day/night temperatures; GR_{50}, effective 2,4-D or glyphosate dose required for 50% biomass reduction of common or giant ragweed; GR_{90}, effective 2,4-D or glyphosate dose required for 90% biomass reduction of common or giant ragweed.

[b] Regression parameters S (slope), L (lower limit), and U (upper limit) of the four-parameter log-logistic model $(Y = L + \{U - L/1 + \exp[S(\log X - \log E)]\})$ were determined by using the nonlinear least-square function of the statistical software R.

[c] The resistance level was determined compared with the field rate of glyphosate (i.e., 1,260 g ae ha^{-1}), because the GS biotypes became too sensitive at the high-temperature regime, leading to instability in the resistance level determined on the basis of the R/S ratio.

Table 3. Goodness of fit (RMSE and EF) of the four-parameter log-logistic model fit to dose–response data including control and biomass reduction in glyphosate-resistant (GR) and glyphosate-susceptible (GS) common and giant ragweed at low- and high-temperature regimes.[a]

	Low temperature (d/n 20/11 C)				High temperature (d/n 29/17 C)			
	Control		Biomass reduction		Control		Biomass reduction	
Herbicide	RMSE	EF	RMSE	EF	RMSE	EF	RMSE	EF
Common ragweed								
2,4-D	12.60	0.83	14.40	0.74	8.62	0.95	11.94	0.82
Glyphosate								
GS biotype	12.03	0.82	13.25	0.82	12.03	0.89	7.62	0.96
GR biotype	9.13	0.83	14.01	0.77	15.8	0.81	18.40	0.68
Giant ragweed								
2,4-D	12.08	0.87	3.06	0.99	1.40	0.99	11.30	0.87
Glyphosate								
GS biotype	9.75	0.93	7.22	0.93	17.60	0.79	10.60	0.85
GR biotype	12.50	0.78	6.25	0.96	7.50	0.94	13.90	0.81

[a] Abbreviations: d/n, day/night temperatures; RMSE, root mean square error; EF, modeling efficiency coefficient.

when d/n temperatures were increased from 18/18 C to 24/18 C or 29/18 C (Jordan et al. 1960). In contrast, Ou et al. (2017) reported reduced efficacy of dicamba, a synthetic auxin herbicide, for control of kochia [*Kochia scoparia* (L.) Schrad.], with a 2- to 4-fold increase in GR_{50} of dicamba at 32.5/22.5 C compared with 25/15 C or 17.5/7.5 C d/n temperature.

The RMSE and EF values for the log-logistic models used for 2,4-D dose–response studies varied from 8.62 to 14.40 and 0.74 to 0.95 (Table 3), respectively, for HT and LT, indicating a good fit. The RMSE and EF values for the dose–response models for giant ragweed varied from 1.40 to 12.08 and 0.87 to 0.99, suggesting good fit compared with common ragweed.

Glyphosate Dose–Response. The efficacy of glyphosate also improved at HT compared with LT for control of GS and GR common or giant ragweed biotypes (Figures 2 and 3). For example, the ED_{50} and ED_{90} values were 437 and 6,963 g ae ha^{-1} at LT compared with 130 and 587 g ae ha^{-1} at HT, respectively, in the GS common ragweed biotype (Table 1). A similar response was reflected in GS common ragweed biomass reduction with the values of GR_{50} and GR_{90} equal to 45 and 1,249 g ae ha^{-1} at LT compared with 39 and 210 g ae ha^{-1} at HT, respectively (Table 2). Likewise, the effective doses of glyphosate for GR common ragweed control were reduced at HT compared with LT, which reduced the level of glyphosate resistance and R/S ratio from 94 and 17 at LT to 6.6 and 14.2 at HT, respectively (Table 1), with similar results for biomass reduction (Table 2).

Lower rates of glyphosate were required for control of GS and GR giant ragweed compared with common ragweed regardless of temperature regime (Tables 1 and 2). For example, the ED_{50} and ED_{90} values for control of GS giant ragweed were 119 and 468 g ae ha^{-1} at LT compared with 62 and 244 g ae ha^{-1} at HT, respectively (Table 1). Similarly, values of GR_{50} and GR_{90} for GS giant ragweed were 59 and 956 g ae ha^{-1} at LT compared with 49 and 154 g ae ha^{-1} at HT, respectively (Table 2). The results of biomass reduction in GR giant ragweed showed a consensus with the control estimates in response to glyphosate at both temperature regimes, and the level of resistance at LT was 52 compared with 4.6 at HT (Tables 1 and 2), signifying that temperature influenced the level of glyphosate resistance. However, in GR giant ragweed, resistance level determined from the ratio of GR_{90} and glyphosate field rate (1,260 g ae ha^{-1}) decreased from 4.7 at LT to 1.8 at HT; though R/S ratio increased from 6.1 at LT to 14.9 at HT due to extreme sensitivity of the GS giant ragweed at HT (Table 2). In similar studies, Jordan (1977) and Reddy (2000) reported an improvement in glyphosate efficacy for control of bermudagrass at 32 C and redvine [*Brunnichia ovata* (Walt.) Shinners] at 35 C compared with 22 C and 25 C, respectively. Additionally, Moretti et al. (2013) reported that the level of glyphosate resistance in hairy fleabane varied depending on whether greenhouse experiments were conducted in summer, fall, or winter.

The RMSE and EF values for models used to analyze the glyphosate dose–response studies of GR and GS common or giant ragweed biotypes indicated an appropriate fit. The RMSE and EF

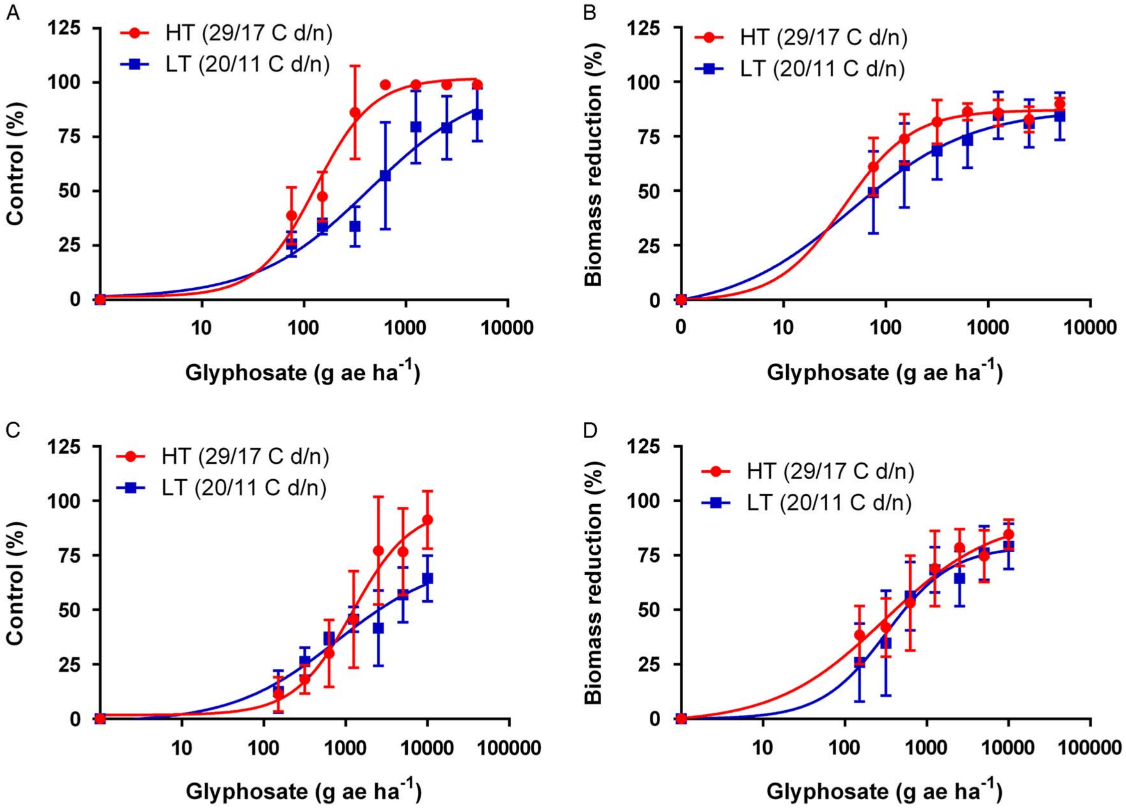

Figure 2. Dose–response curves of glyphosate-susceptible (GS) and glyphosate-resistant (GR) common ragweed biotypes to glyphosate applied at high temperature (HT) and low temperature (LT) regimes at 21 d after treatment: (A) control of GS common ragweed, (B) biomass reduction of GS common ragweed, (C) control of GR common ragweed, and (D) biomass reduction of GR common ragweed.

values for dose–response models in GS common ragweed varied from 7.62 to 13.25 and 0.82 to 0.96 compared with 9.13 to 18.40 and 0.68 to 0.83 in GR common ragweed, respectively (Table 3). Similarly, RMSE and EF values for the giant ragweed dose–response study ranged from 9.75 to 17.60 and 0.78 to 0.96, respectively (Table 3). These values indicated that the prediction models were fitting well to the data and were comparable with the goodness-of-fit parameters reported by Ganie and Jhala (2017) for glyphosate dose–response in GR and GS common ragweed.

2,4-D Absorption and Translocation. Absorption was not affected but the translocation of [^{14}C]2,4-D and/or its derivatives varied with temperature in common ragweed and giant ragweed biotypes (Figure 4). For example, in a period of 24 to 96 HAT, mean absorption of [^{14}C]2,4-D in common ragweed increased from 17% to 40% and 20% to 35% at LT and HT, respectively (Figure 4A). In contrast, [^{14}C]2,4-D absorption increased from 30% to 58% at LT and 20% to 62% at HT in giant ragweed in a similar time period (Figure 4C). However, translocation of [^{14}C]2,4-D and/or its derivatives was greater at HT compared with LT in both common and giant ragweed biotypes, likely contributing to improved efficacy at HT. Mean translocation in common ragweed reached 54% of the absorbed [^{14}C]2,4-D at HT compared with 35% at LT at 96 HAT (Figure 4B). Similarly, 45% of the absorbed [^{14}C]2,4-D was translocated in giant ragweed at HT compared with 27% at LT at 96 HAT (Figure 4D). Increased translocation to plant parts above and below the treated leaf occurred at HT compared with LT (unpublished data). In the same way, increased absorption and translocation of 2,4-D was observed in kidney beans with increasing temperatures from 20 to 30 C (Pallas 1960). In contrast, Schultz and Burnside (1980) reported similar translocation of 2,4-D varying from 35% to 39% at 25 and 30 C in hemp dogbane (*Apocynum cannabinum* L.).

Glyphosate Absorption and Translocation. Mean absorption of [^{14}C]glyphosate (as % applied) increased from 49% to 64% at LT compared with 41% to 55% at HT in GS common ragweed in a period of 24 to 96 HAT (Figure 5A). However, translocation of absorbed [^{14}C]glyphosate reached

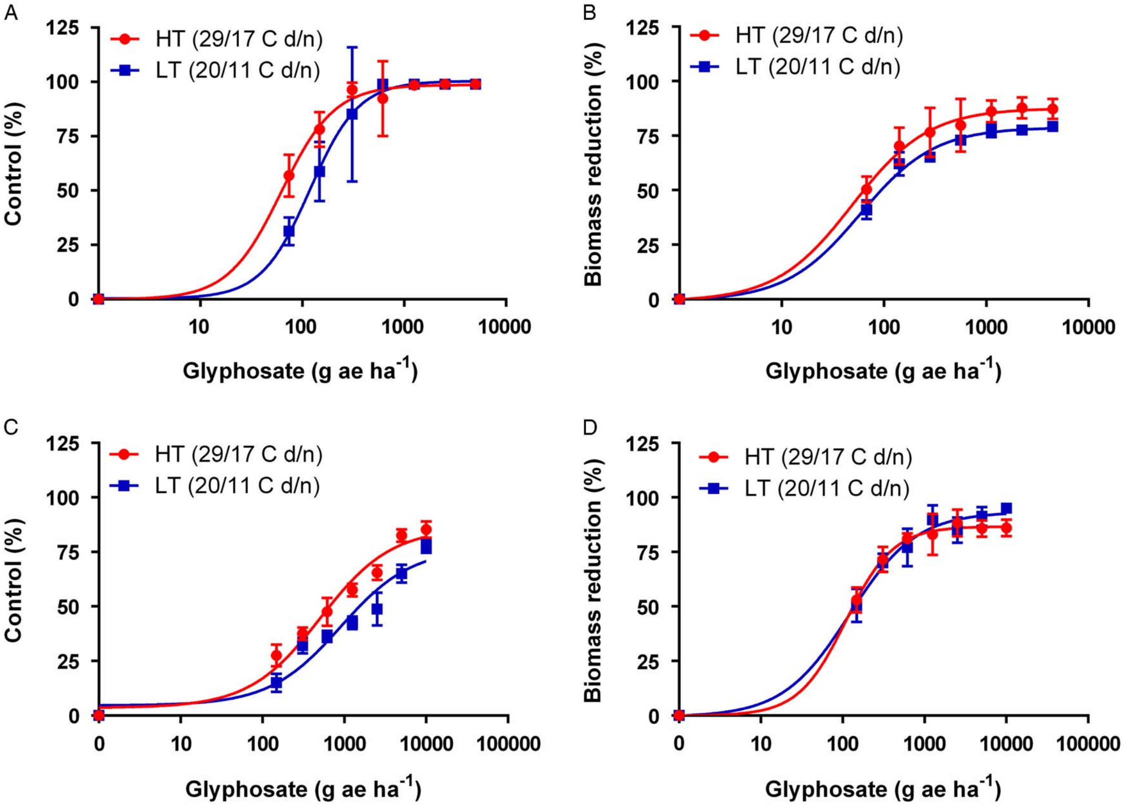

Figure 3. Dose–response curves of glyphosate-susceptible (GS) and glyphosate-resistant (GR) giant ragweed biotypes to glyphosate applied at high temperature (HT) and low temperature (LT) regimes at 21 d after treatment: (A) control of GS giant ragweed, (B) biomass reduction of GS giant ragweed, (C) control of GR giant ragweed, and (D) biomass reduction of GR giant ragweed.

54% at HT compared with 35% at LT at 96 HAT (Figure 5B). In contrast, the absorption of [^{14}C] glyphosate in GS giant ragweed varied from 18% to 54% at HT compared with 11% to 40% at LT (Figure 6A). At 96 HAT, 69% of the absorbed [^{14}C] glyphosate was translocated at HT compared with 50% at LT in GS giant ragweed (Figure 6B). Thus, the absorbed [^{14}C]glyphosate was translocated more in common ragweed at HT compared with LT. However, in giant ragweed, increased absorption and translocation was observed at HT compared with LT at 96 HAT. Similarly, Schultz and Burnside (1980) also reported that translocation of glyphosate increased from 18% at 25 C to 39% at 30 C in hemp dogbane. Likewise, Reddy (2000) reported an increased absorption and translocation of glyphosate in redvine at a d/n temperature of 35/30 C compared with 25/20 or 15/10 C.

Results of glyphosate dose–response studies suggested decreasing levels of resistance at HT compared with LT in GR common or giant ragweed biotypes from Nebraska. The mean absorption of [^{14}C] glyphosate in GR common ragweed was unaffected by temperature and increased from 47% to 60% at LT compared with 39% to 60% at HT in a period of 24 to 96 HAT (Figure 5C). In contrast, higher [^{14}C] glyphosate translocation was observed in GR common ragweed at HT varying from 25% to 41% compared with 17% to 33% at LT (Figure 5D). Likewise, the mean absorption of [^{14}C]glyphosate in GR giant ragweed increased from 15% to 34% at HT and 15% to 23% at LT (Figure 6C). However, translocation of the absorbed [^{14}C]glyphosate increased from 22% to 41% at HT compared with 12% to 44% at LT in GR giant ragweed (Figure 6D). Increased absorption and/or translocation of [^{14}C]glyphosate reduced the level of glyphosate resistance in GR common and giant ragweed biotypes at HT compared with LT; however, resistance was not overcome, as the effective glyphosate rates required for 90% control were much higher compared with the labeled rate (Tables 1 and 2). Pline et al. (1999) reported that resistance in GR soybeans decreased at 35 C due to increased translocation of glyphosate to the meristematic regions compared with 15 or 25 C.

Results indicate increased efficacy of 2,4-D or glyphosate for control of common or giant ragweed at HT compared with LT and reduced levels of

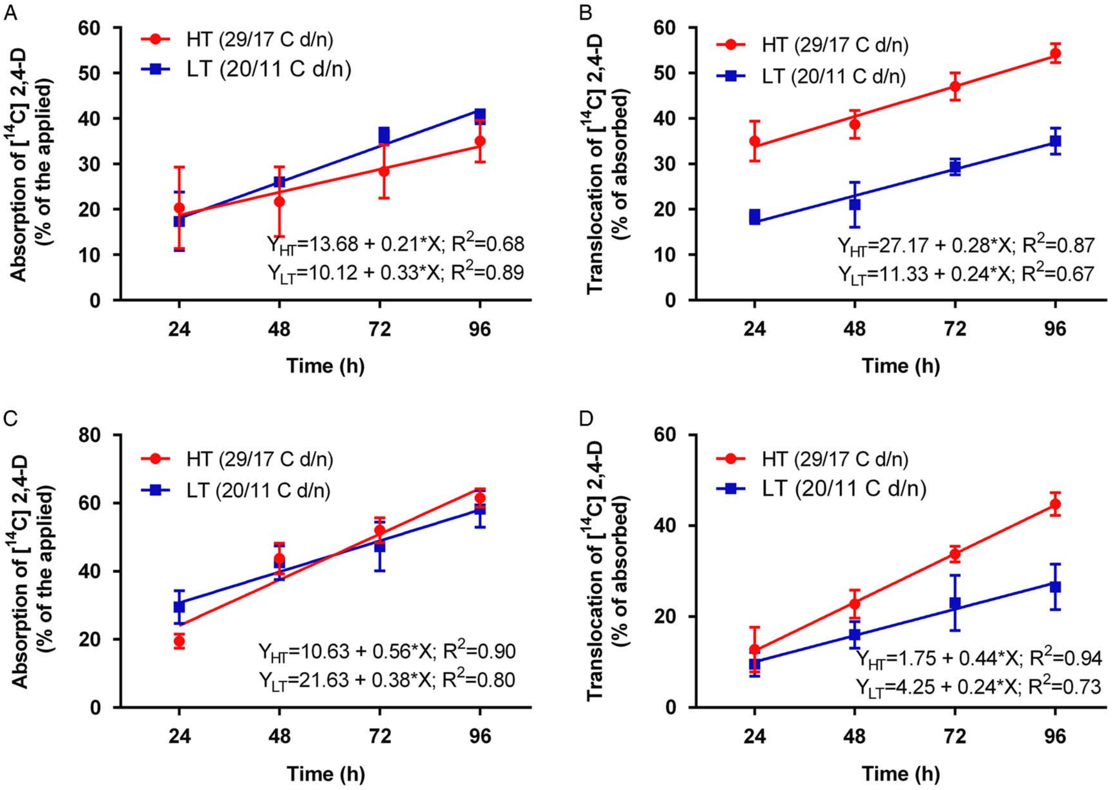

Figure 4. Absorption and translocation of 2,4-D in common and giant ragweed with time at high temperature (HT) and low temperature (LT) regimes: (A) 2,4-D absorption in common ragweed, (B) translocation of 2,4-D and/or its derivatives in common ragweed, (C) 2,4-D absorption in giant ragweed, and (D) translocation of 2,4-D and/or its derivatives in giant ragweed.

glyphosate resistance in GR common and giant ragweed at HT (Tables 1 and 2). Earlier research has suggested that absorption and translocation of the systemic herbicides might be enhanced at high temperatures due to the effect on herbicide penetration facilitated by physicochemical factors, including increased rate of diffusion, reduced viscosity of the cuticle, and physiological factors comprising increases in photosynthesis, phloem translocation, and protoplasmic streaming (Currier and Dybing 1959). Increased growth temperatures modify the characteristics of leaf cuticular wax (Hess and Falk 1990; Willingham and Graham 1988) and enhance the cuticle and plasma membrane fluidity, resulting in improved herbicide absorption and translocation (Johnson and Young 2002).

The absorption and translocation of 2,4-D in this study suggested that increased translocation possibly contributed to the higher efficacy in common and giant ragweed at HT compared with LT. Several studies reported improved efficacy of 2,4-D with increasing temperature in certain species, including common duckweed (*Lemna minor* L.) (Blackman and Robertson-Cunninghame 1955), buckhorn plantain (*Plantago lanceolata* L.) (Marth and Davis 1945), flax (Jordan et al. 1960), and kidney beans (Pallas 1960). However, the mechanism(s) for increased efficacy of 2,4-D at warmer temperatures has not been thoroughly studied; nonetheless, slower uptake and translocation combined with detoxification of 2,4-D were suspected as possible mechanisms for reduced efficacy at lower temperatures in coast fiddleneck [*Amsinckia menziesii* (Lehm.) A. Nels. & J.F. Macbr. var. intermedia (Fisch. & C.A. Mey.) Ganders] (Muzik and Mauldin 1964). Similarly, greater efficacy of glyphosate at HT compared with LT in this study can be attributed to increased translocation in common ragweed and increased absorption and translocation in giant ragweed. Likewise, Schultz and Burnside (1980) reported reduced tolerance to glyphosate in hemp dogbane at 30 C compared with 25 C due to increased translocation at 30 C. Earlier studies have reported that the increase in glyphosate absorption with rise in temperature resulted in greater phytotoxicity at warmer temperature compared with lower temperature regimes in potato (*Solanum tuberosum* L.) (Masiunas and Weller 1988). Furthermore, increasing glyphosate absorption and translocation with rise in temperature has been reported in johnsongrass (McWhorter et al. 1980).

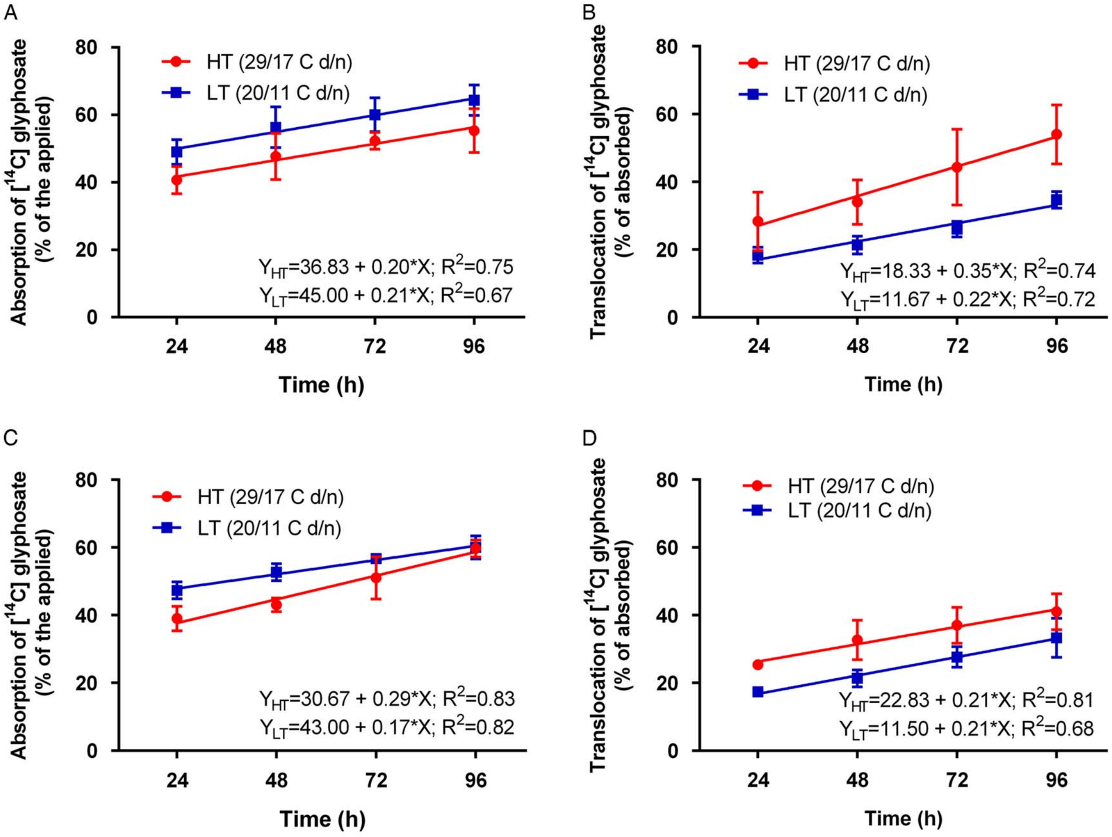

Figure 5. Absorption and translocation of glyphosate in glyphosate-susceptible (GS) and glyphosate-resistant (GR) common ragweed with time at high temperature (HT) and low temperature (LT) regimes: (A) glyphosate absorption in GS common ragweed, (B) glyphosate translocation in GS common ragweed, (C) glyphosate absorption in GR common ragweed, and (D) glyphosate translocation in GR common ragweed.

Practical Implications. The findings of this research revealed the effect of temperature on the efficacy, absorption, and translocation of 2,4-D or glyphosate for control of GR and GS common and giant ragweed. Common and giant ragweed were more sensitive to 2,4-D or glyphosate at higher temperatures; therefore, temperature should be considered when determining the proper time of application, specifically when applying preplant in early spring in Nebraska, where the temperature can fluctuate dramatically. Stopps et al. (2013) reported that glyphosate efficacy on velvetleaf (*Abutilon theophrasti* Medik.), Amaranthus spp., and common ragweed increased when treatments were applied between noon and 6 pm, which corresponds to the maximum air temperatures observed during the day. Applications of 2,4-D or glyphosate should be scheduled during warmer days (>20 C or ≈29 C) to improve efficacy. In addition, temperature forecasts for the days following herbicide application should be warmer for improved efficacy. This study was conducted under growth-chamber conditions with precise temperature regimes and constant relative humidity; therefore, the results may vary under field conditions due to the complex interaction among environmental factors, including fluctuations in temperature, relative humidity, wind, light, etc. (Varanasi et al. 2016). Future studies should be conducted to evaluate the integrated effect of temperature and other environmental factors such as light and relative humidity on herbicide efficacy. Moreover, molecular studies, including changes in plant metabolism and gene expression with varying environmental factors, may reveal more evidence to explain the physiological mechanisms involved with the variable response.

Acknowledgments

The authors wish to thank the Indian Council of Agricultural Research, New Delhi, India for partial financial support to the first author (ZAG) and the U.S. Department of Agriculture National Institute of Food and Agriculture Hatch fund. We appreciate the help of Junjun Ou, Kansas State University, in this project.

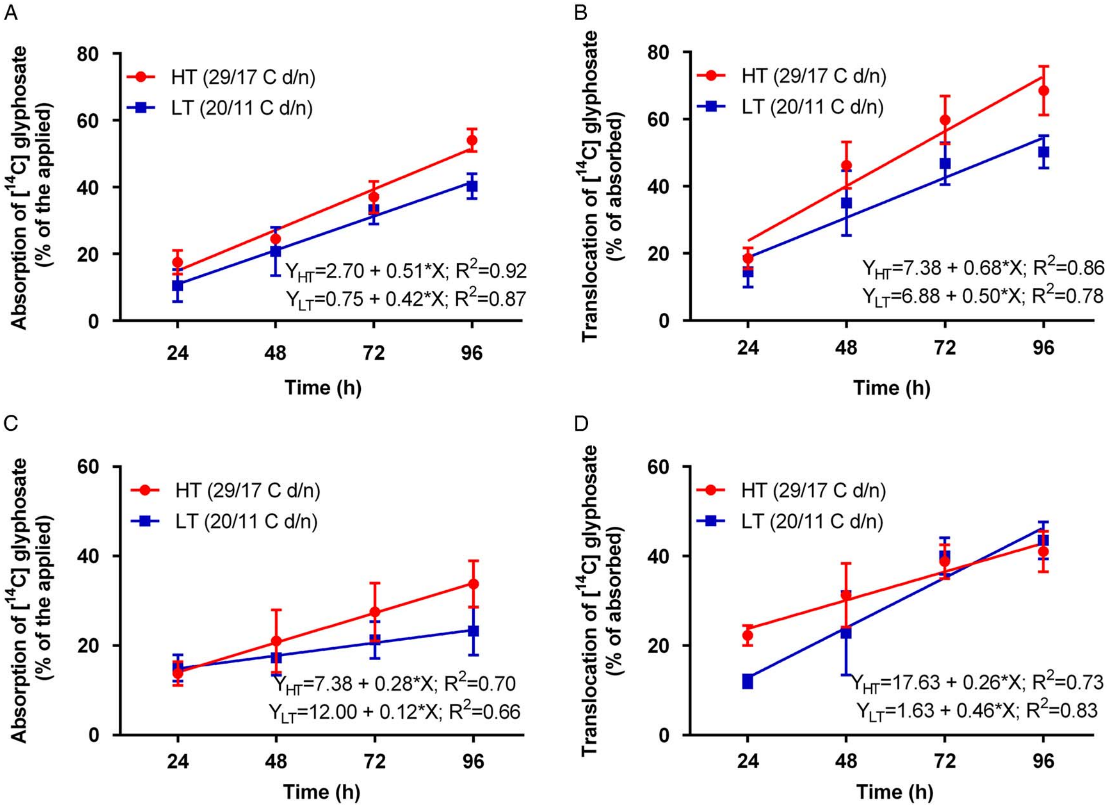

Figure 6. Absorption and translocation of glyphosate in glyphosate-susceptible (GS) and glyphosate-resistant (GR) giant ragweed with time at high temperature (HT) and low temperature (LT) regimes: (A) glyphosate absorption in GS giant ragweed, (B) glyphosate translocation in GS giant ragweed, (C) glyphosate absorption in GR giant ragweed, and (D) glyphosate translocation in GR giant ragweed.

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Received February 21, 2017, and approved May 5, 2017.

Associate Editor for this paper: Dean Riechers, University of Illinois.