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ARTICLE

Growth and seed production of glyphosate-resistant giant ragweed (*Ambrosia trifida* L.) in response to water stress

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Abstract: The objectives of this study were to determine the effects of degree and duration of water stress on growth and seed production of glyphosate-resistant (GR) giant ragweed. The degree of water stress included giant ragweed response to 100%, 75%, 50%, 25%, and 12.5% of field capacity. The highest growth index (588 cm^3) was achieved at 75% of field capacity with plants typically ≥125 cm tall and ≥57 leaves $plant^{-1}$. Giant ragweed seed production was ≥55, 35, 20, and 5 seeds $plant^{-1}$ at ≥75%, 50%, 25%, and 12.5% of field capacity, respectively. The study of duration of water stress included the response of giant ragweed to withholding water for 2, 4, 6, 8, and 10 d following 100% of field capacity. Water stress of 4 d or longer reduced giant ragweed plant height ≥20%, root and shoot biomass ≥66%, number of leaves ≥36%, growth index ≥54%, and seed production by 36% compared with 2 d of water stress. Results from this study indicate that giant ragweed can survive and produce seeds at 12.5% of field capacity or 10 d of water stress.

Key words: Aboveground biomass, degree of water stress, duration of water stress, growth index, root biomass.

Résumé : L'étude devait établir les effets de l'intensité et de la durée du stress hydrique sur la croissance et la reproduction de la grande herbe à poux résistante au glyphosate. L'intensité du stress hydrique correspondait à la réaction de l'adventice à 100, 75, 50, 25 et 12,5 % de la capacité de rétention. L'indice de croissance le plus élevé (588 cm^3) a été observé à 75 % de la capacité de rétention, les plants mesurant habituellement 125 cm ou davantage et comptant 57 feuilles ou plus par spécimen. La grande herbe à poux produit respectivement ≥ 55, 35, 20 et 5 graines par plant à ≥ 75, 50, 25 et 12,5 % de la capacité de rétention. L'étude sur la durée du stress hydrique portait sur la réaction de l'adventice à 2, 4, 6, 8 ou 10 jours de sécheresse après qu'une capacité de rétention maximale a été atteinte. Un stress hydrique de quatre jours ou plus réduit la taille de la grande herbe à poux de ≥ 20 %, la biomasse de ses racines et de ses pousses de ≥ 66 %, le nombre de feuilles de ≥ 36 %, l'indice de croissance de ≥ 54 % et la production de graines de 36 %, comparativement à un stress de deux jours. Les résultats indiquent que la grande herbe à poux peut survivre et se reproduire à une capacité de rétention de 12,5 % ou après dix jours de sécheresse. [Traduit par la Rédaction]

Mots-clés : biomasse aérienne, intensité du stress hydrique, durée du stress hydrique, indice de croissance, biomasse des racines.

Introduction

Giant ragweed (*Ambrosia trifida* L.) is a problematic, early emerging summer annual weed in agronomic crops, and is also found in drainage ditches, roadsides, and other non-agricultural areas (Johnson et al. 2006). Giant ragweed is native to North America and is widely distributed throughout the United States and eastern Canada (Barnett and Steckel 2013; Bassett and Crompton 1982). It has been rated among the 10 most expensive to manage agricultural weeds in the U.S. states of Minnesota, Nebraska, and Ohio (Jordan 1985; Loux and Berry 1991). Giant ragweed emergence begins in late March and continues until early summer (end of May) (Davis et al. 2013; Werle et al. 2013, 2014; Kaur et al. 2016); however, its emergence pattern can vary according to region. For instance, a late-season giant ragweed escape has been documented in 20% of soybean fields in Indiana (Johnson et al. 2004). Early and

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Abbreviations: GR, glyphosate-resistant; **POST**, post-emergence; **PRE**, pre-emergence; **WAT**, week after treatment.

prolonged emergence patterns of giant ragweed make it a highly competitive weed for light, nutrients, and moisture (Abul-Fatih and Bazzaz 1979*a*; Gibson et al. 2005). Giant ragweed competition in corn (*Zea mays* L.) (Harrison et al. 2001), cotton (*Gossypium hirsutum* L.) (Barnett and Steckel 2013), and soybean [*Glycine max* (L.) Merr.] (Webster et al. 1994) has been reported to cause a 10%–75% reduction in yield, depending on the density and the crop.

Indiscriminate use of glyphosate in glyphosate-tolerant crops over the past 20 years has led to the evolution of GR giant ragweed in 12 states in the US, including Nebraska (Heap 2015), and in Ontario, Canada (Vink et al. 2011). The post-emergence (POST) control of GR giant ragweed is challenging in glyphosate-tolerant crops, including corn and soybean, due to a limited number of effective POST herbicides (Steckel 2007; Steckel et al. 2011; Jhala et al. 2014; Kaur et al. 2014). Norsworthy et al. (2011) reported that differential absorption or translocation was not a mechanism of glyphosate-resistance in giant ragweed biotypes from Arkansas. Additionally, studies were conducted with all possible mechanisms of glyphosate-resistance in common ragweed (*Ambrosia artemisiifolia* L.), a closely related species of giant ragweed, from Nebraska suggest that the mechanism is unknown and more research is needed (Ganie et al. 2016).

Giant ragweed seeds undergo physiological and covering structure enforced dormancy (Schutte et al. 2012). To break dormancy, seeds require cold stratification, which is achieved in nature by overwintering seeds under cool and moist soil conditions (Ballard et al. 1996). Giant ragweed seeds are relatively large (0.5–1.1 cm) and store a sufficient amount of food reserves to increase seedling tolerance to stress factors and promote emergence from greater depths (Abul-Fatih and Bazzaz 1979*b*; Harrison et al. 2007). Compared with other annual weed species, such as common waterhemp (*Amaranthus rudis* Sauer) (Wu and Owen 2014) and common lambsquarters (*Chenopodium album* L.) (Colquhoun et al. 2001), giant ragweed has relatively low fecundity and seed survival rate (Harrison et al. 2001).

A study to determine the fitness of GR and susceptible giant ragweed biotypes from Indiana suggested that the GR biotype flowered earlier and produced 25% less seed than the susceptible biotype (Brabham et al. 2011). In contrast, Glettner and Stoltenberg (2015) reported that the growth and development of GR giant ragweed was similar to the susceptible biotype. The viability and germination of giant ragweed seeds depend on several factors, including seed burial depth, soil temperature, and available moisture (Abul-Fatih and Bazzaz 1979*b*; Stoller and Wax 1974; Harrison et al. 2007). Wortman et al. (2012) reported that summer seed survival of giant ragweed ranged between 0.8% to 85% depending on site/year and precipitation in several Corn Belt states, greater than the seed survival rates observed by Harrison et al. (2007), which ranged from 0% to 34% after 1 yr depending on seed size and burial depth.

Environmental stresses prevent plants from achieving optimum growth potential and affect fecundity (Patterson 1995). Water stress is one of the most important biotic factors that significantly reduce crop yields depending on level of stress (Boyer 1982). Saini and Aspinall (1981) reported that water stress had a negative effect on pollen production and fertility in wheat (*Triticum aestivum* L.) that reduced seed production. Westcott and Jewison (2012) reported significant reduction in corn and soybean yields due to drought, indicating that water deficit conditions during critical stages of plant growth can reduce crop productivity. Water stress also reduced height, weight, and leaf area in vegetable amaranth (*Amaranthus viridis* L.) (Liu and Stutzel 2002), and Kishor et al. (1995) reported leaf wilting and decreased water potential in transgenic tobacco (*Nicotiana tabacum* L.).

Response to water stress has been studied in a limited weed species. For example, Chauhan (2013) reported a significant decline in seed production in itchgrass [*Rottboellia cochinchinensis* (Lour.)], i.e., 560 and 9 seeds plant^{-1} at 75% and 12.5% of field capacity, respectively. Similarly, 4-fold less seed production has been reported at 12.5% compared with 100% field capacity in junglerice (*Echinochloa colona* L.) (Chauhan and Johnson 2010), and reductions in plant height, biomass, and seed production with increased durations of water stress were reported. It was further found that junglerice was more vigorous than rice (*Oryza sativa* L.) when grown together under water stress conditions. Webster and Grey (2008) showed a linear relationship between water volume and seed production in Benghal dayflower (*Commelina benghalensis* L.), indicating that water deficiency inhibits growth and reproduction. Geddes et al. (1979) further reported that common cocklebur (*Xanthium strumarium* L.) exploited a greater volume of soil for water than soybean in a field study to evaluate water extraction and the water use efficiency of common cocklebur and soybean grown under competition. To evaluate the effect of giant foxtail (*Setaria faberii* Herrm.) density on soybean yield, Hahn (1986) reported that yield losses were higher in a year of greater rainfall compared with a dry year (Hahn 1986), indicating the impact of water stress on crop-weed competition.

Water deficit in terms of degree and duration is seldom positively associated with a plant's growth and fecundity. Scientific literature is not available on whether giant ragweed plants are able to grow and produce seeds under water-stressed conditions. The objectives of this study were to determine the effects of degree and duration of water stress on the growth and seed production of GR giant ragweed.

Table 1. Regression parameters of a four-parameter logistic model[a] fitted to glyphosate-resistant giant ragweed plant height, number of leaves, and growth index at different degree of water stress treatments in a greenhouse experiment conducted at the University of Nebraska-Lincoln.

Field capacity	*b*	*D*[b,c]	*e*	*b*	*D*[b,c]	*e*	*b*	*D*[b,c]	*e*
%	Plant height (cm)			Leaves plant^{-1}			Growth index[d] (cm^3)		
100	−1.5 (0.5)	125 (24.4) ab	6 (1.9)	2.4 (1.1)	57 (10.9) a	7 (1.5)	−3.7 (1.5)	416 (29.5) b	4 (0.5)
75	−1.6 (0.4)	140 (22.1) a	6 (1.6)	1.4 (0.8)	58 (30.6) a	9 (7.2)	−2.3 (0.9)	588 (95.2) a	6 (1.3)
50	−1.5 (0.3)	112 (13.1) b	6 (1.1)	1.5 (0.6)	39 (10.4) a	6 (2.7)	−7.2 (6.8)	274 (13) c	4 (0.5)
25	−1.6 (0.5)	69 (9.2) c	5 (1.0)	2.1 (2.6)	16 (2.6) b	2 (0.5)	−16.2 (53)	128 (6.7) d	4 (1.6)
12.5	−1.9 (0.4)	32 (3.5) d	2 (0.9)	2.7 (2.9)	7 (1.3) b	18 (5.2)	0	32 (3.5) e	2 (0.9)

[a] $Y = C + \{D - C / 1 + \exp[B(X - E)]\}$, where *Y* is the plant height, leaves plant^{-1}, or growth index at time X (week after transplanting); C is the lower limit considered as 0; *D* is the estimated maximum plant height, number of leaves, or growth index; E is the time taken to reach 50% of final height, number of leaves, or growth index; and *B* is the relative slope around the parameter E.

[b] Values in parenthesis are standard error of mean.

[c] Means within columns with no common letter(s) are significantly different according to Fisher's Protected LSD test at $P \leq 0.05$.

[d] Growth index $= \pi \times (w/2)^2 \times h$; where *w* is the plant girth calculated as an average of two girths, one measured at the widest point and another perpendicular to the first; and *h* is the plant height.

Materials and Methods

Plant material

Seeds of a GR giant ragweed biotype were collected in fall 2012 from David City, Nebraska, USA (41.25°N, 97.13°W) and were stored in a freezer (0° C) for 4 mo. The giant ragweed biotype from this site was confirmed resistant to glyphosate in 2011, with the level of resistance ranging from 14x to 36x (x is the recommended rate of glyphosate at 870 g ae ha^{-1}) compared with susceptible biotypes depending on plant height (Rana et al. 2013). Seeds were packed in mesh bags and stratified by placing them between layers of a mixture of potting mix and soil (3:1) in a plastic box measuring 58 cm × 42 cm × 15 cm. The plastic boxes were kept in a freezer for 3 mo to break seed dormancy. Seeds were removed from the freezer and sown in cell plug trays measuring 53 cm × 26 cm × 6 cm. After emergence, when seedlings were 5 cm tall, they were transplanted into free-draining pots (26 cm in diameter and 48 cm deep).

Field capacity

Field capacity was calculated to determine the amount of water needed to simulate soil moisture levels at respective water stress treatments. The soil used in this study was collected from a field near Lincoln, Nebraska, USA with no history of residual herbicide application for the last 5 yr. Air-dried soil was passed through a 3 mm sieve to achieve a uniform consistency. The soil type was a silt-loam (25% clay, 24% sand, and 51% silt) with a pH of 6.1, 1.38 g cm^{-3} bulk density, and 2.8% organic matter. Each pot was filled with 10 kg of dry soil, and field capacity was determined by modifying the method described by Steadman et al. (2004). First, the weight of the pots containing dry soil was measured, and then the pots were watered to saturation and covered with shiny paper sheets to minimize evaporation. Pots were allowed to drain freely for 36 h to establish the amount of water needed to maintain soil moisture levels at respective field capacity. Pots were re-weighed to calculate the percent field capacity using the equation:

$$\text{Field capacity}\ (\%) = [(W_w - W_d)/d] \quad (1)$$

where W_w is the wet weight of the soil along with the pot, W_d is the dry weight of the soil along with the pot, and d is the density of water (i.e., 1 g cm^{-3}).

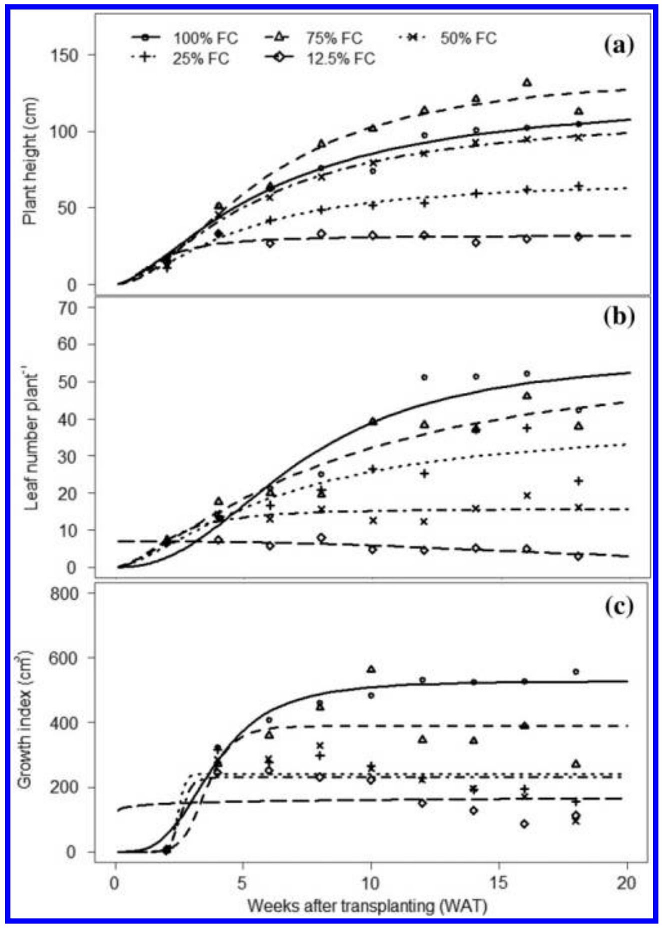
Experimental setup

Modifying the procedures explained by Webster and Grey (2008), Chauhan and Johnson (2010), and Chauhan (2013), two separate experiments were conducted in the greenhouse at the University of Nebraska-Lincoln to determine the response of GR giant ragweed to water stress conditions. The first experiment included degree of water stress treatments: 12.5% (severe stress), 25% (high stress), 50% (moderate stress), 75% (light stress), and 100% (no stress). The required volume of water was applied every 2 d. In the second experiment (duration of water stress), five durations of water stress treatments were maintained: 2, 4, 6, 8, and 10 d of water stress at 100% of field capacity.

To determine an effective interval for withholding water from the giant ragweed plants to establish different degrees of water stress, a preliminary experiment was conducted in the greenhouse. The study consisted of five treatments of 1, 2, 3, 4, and 5 d of water stress in pots in a randomized complete block design with six replications. Six benches in the greenhouse were used as a replicate. The experiment was repeated in time. In each treatment, water was applied at 100% of field capacity at 1, 2, 3, 4, or 5 d intervals. Plant height, number of leaves plant^{-1}, and aboveground biomass were measured at 45 d after transplanting (DAT). The results showed that the plants treated with 100% of field capacity at a 2 d interval resulted in maximum plant height, number of leaves plant^{-1}, and aboveground biomass compared with other water stress intervals (data not shown); therefore, the 2 d interval was selected for the degree of water stress study to apply the desired degree of water stress treatments.

To include exclusively GR giant ragweed plants in this study, glyphosate (Touchdown HiTech®, Syngenta Crop Protection, LLC, Greensboro, NC) was applied at 1050 g ae ha^{-1} when giant ragweed plants were 8- to 10-cm tall using a single-tip chamber sprayer (DeVries Manufacturing Corp, Hollandale, MN 56045) fitted with an 8001 E nozzle (TeeJet, Spraying Systems Co., Wheaton, IL 60187) calibrated to deliver 140 L ha^{-1} spray volume at 207 kPa. Glyphosate treatment was prepared in distilled water and mixed with nonionic surfactant (NIS, Induce, Helena Chemical Co., Collierville, TN) at 0.25% *v*/*v*, and ammonium sulfate (AMS, DSM Chemicals North America Inc., Augusta, GA) at 2.5% *w*/*v*. Giant ragweed plants that survived glyphosate application were used in this study and glyphosate-susceptible plants were discarded. Pots in both experiments were arranged in a randomized complete block design with five replications. Both experiments were repeated under the same greenhouse conditions at temperature ranges 22 °C–28 °C. The first greenhouse experiment was started in March 2013 and the second experiment was started (repeated) in April 2014 with the same procedure. Metal halide lamps with 600 μmol photon m^{-2} s^{-1} light intensity provided supplemental light in the greenhouse to ensure a 14 h photoperiod.

Fig. 1. Effect of degree of water stress on glyphosate-resistant giant ragweed (*a*) plant height, (*b*) leaf number, and (*c*) plant volume at 2–18 WAT in a greenhouse study conducted at the University of Nebraska–Lincoln. Abbreviations: FC, field capacity; WAT, weeks after transplanting.



Data collection

Data were recorded for plant height, number of leaves per plant, and growth index at 14 d intervals until giant ragweed maturity in both experiments. Growth index (GI) was calculated using the equation (Irmak et al. 2004; Dhir and Harkess 2011)

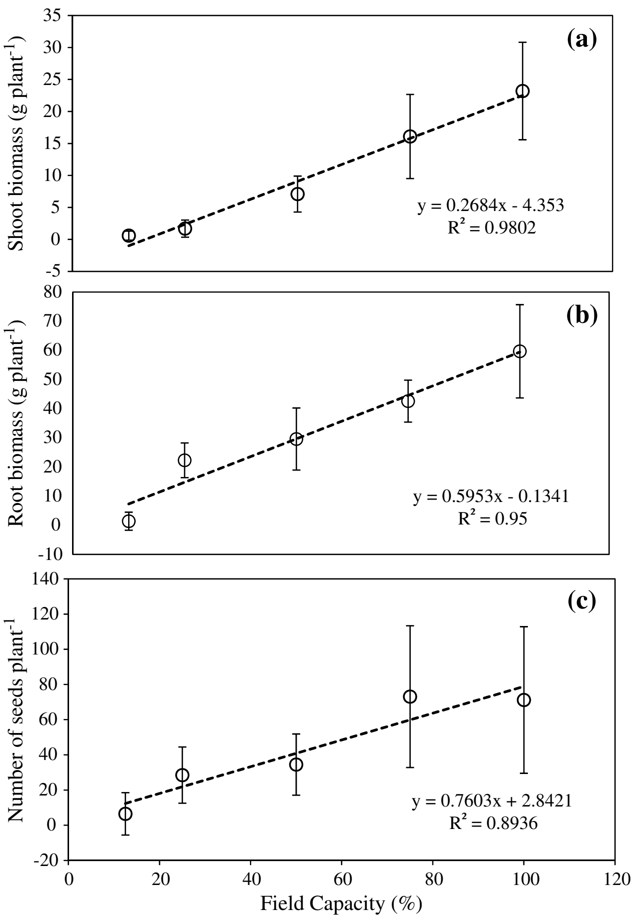
$$\text{Growth Index}\,(\text{cm}^3) = \pi \times (w/2)^2 \times h \qquad (2)$$

where w is the width of the plant calculated as an average of two plant girths, one measured at the widest point and another perpendicular to the first; and h is the plant height measured from the soil surface to the last stem-node at the top (Dhir and Harkess 2011). The volume occupied by the plant was estimated as a cylinder. After 18 wk of transplanting, plants were removed from the pots and their roots were gently washed to remove soil particles. Roots, stems, and leaves were separated, placed in separate paper bags, oven-dried at 65 °C for 72 h, and shoot and root biomass were determined. Seeds were harvested manually and the total number of seeds produced by each plant was counted.

Statistical analyses

Data were subjected to ANOVA. The UNIVARIATE procedure was used to test data for normality and homogeneity of variance. To satisfy the assumptions of normality and homogeneity of variance, plant height, root biomass, and shoot biomass data were log transformed; data on number of leaves, seed number, and growth index were arcsine square root transformed for both experiments (degree and duration of water stress). Experimental run, treatment, and their interaction were considered fixed effects and replication was the random effect in the model using the PROC MIXED procedure in SAS (SAS Institute, Cary, NC). Treatment effects compared on the transformed scale were converted back to the original scale for presentation of results. Data from different experimental runs were combined because there was no significant treatment-by-experiment

Fig. 2. Effect of degree of water stress on giant ragweed (*a*) shoot biomass, (*b*) root biomass, and (*c*) seed production at 18 WAT in a greenhouse study conducted at the University of Nebraska–Lincoln. The vertical bars represent standard error of means (n = 10). Abbreviation: WAT, week after transplanting. The data were regressed using linear model as: $Y = a + bx$, where Y is shoot or root dry biomass or number of seeds plant^{-1}, a is the intercept, b is the slope of the curve, and x is the field capacity.



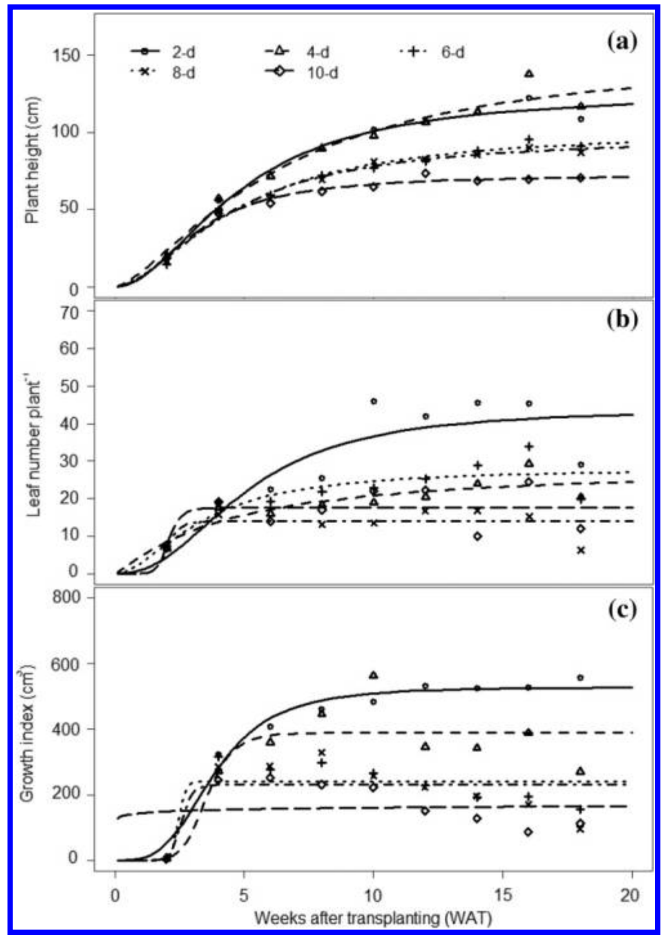
interaction. A linear model was fitted to regress shoot and root biomass, and number of seeds plant^{-1} over different water stress treatments.

$$Y = a + bx \quad (3)$$

where Y is shoot or root dry biomass or number of seeds plant^{-1}, a is the intercept, b is the slope of the curve, and x is the degree or duration of water stress.

Data for plant height, number of leaves plant^{-1}, and growth index were regressed over degree and duration of water stress treatments using a four-parameter logistic model using the *drc* package (drc 1.2, Christian Ritz and Jens Strebig, R2.5, Kurt Hornik) in software R (R statistical software, R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org) (Seefeldt et al. 1995; Knezevic et al. 2007),

Fig. 3. Effect of duration of water stress on glyphosate-resistant giant ragweed (*a*) plant height, (*b*) leaf number, and (*c*) growth index at 2–18 WAT in a greenhouse study conducted at the University of Nebraska–Lincoln. Abbreviation: WAT, week after transplanting.



$$Y = C + \{D - C/1 + \exp[B(X - E)]\} \quad (4)$$

where Y is the response variable (plant height, leaves plant^{-1}, or growth index), C is the lower limit considered as 0, D is the upper limit, B is the slope, E is the time to reach 50% of the maximum value of the response variable, and X is water stress in terms of degree or duration.

Results and Discussion

Degree of water stress

The degree of water stress treatments affected giant ragweed plant height (P = 0.002), number of leaves (P = 0.01), and seed production (P = 0.002). Plant height followed a sigmoid pattern with a maximum height of 140 cm at 16 wk after transplanting (WAT) at 75% of field capacity and did not differ from 100% field capacity (Table 1). This might be because the moisture requirement of giant ragweed plants might be sufficient to provide maximum plant growth at 75% field capacity. In field situations, the crops may suffer from water stress at reduced field capacity and giant ragweed may grow

Table 2. Regression parameters of a four-parameter logistic model[a] fitted to glyphosate-resistant giant ragweed plant height, number of leaves, and growth index at different duration of water stress treatments in a greenhouse experiment conducted at the University of Nebraska-Lincoln.

Duration of water stress	*b*	$D^{b,c}$	*e*	*b*	$D^{b,c}$	*e*	*b*	$D^{b,c}$	*e*
Days	Plant height (cm)			Leaves plant^{-1}			Growth index[d] (cm^3)		
2	−1.9 (0.3)	127 (3.9) b	5 (0.6)	−2.3 (1.1)	44 (5.1) a	5 (0.9)	−3.4 (1.3)	529 (36.6) a	4 (0.5)
4	−1.5 (0.4)	152 (13) a	6 (2.1)	−2.3 (0.9)	29 (14.7) ab	4 (4.5)	−7.1 (9.3)	390 (30.3) b	4 (0.7)
6	−1.7 (0.5)	102 (5.1) c	5 (1.0)	−7.3 (6.7)	28 (4.9) b	3 (1.0)	−19.2 (49.1)	241 (14.3) c	3 (1.4)
8	−1.8 (0.3)	97 (2.6) c	4 (0.5)	−16.2 (52.5)	14 (0.5) bc	2 (0.1)	−12.5 (8.5)	231 (12.4) c	3 (0.5)
10	−2.1 (0.6)	74 (1.9) d	3 (0.4)	−2.7 (2.9)	18 (1.4) bc	2 (0.2)	−0.1 (0.1)	210 (1.2) c	3 (0.7)

[a]$Y = C + \{D - C / 1 + \exp[B(X - E)]\}$, where *Y* is the plant height, leaves plant^{-1}, or growth index at time X (week after transplanting); C is the lower limit considered as 0; *D* is the estimated maximum plant height, number of leaves, or growth index; E is the time taken to reach 50% of final height, number of leaves, or growth index; and *B* is the relative slope around the parameter *E*.

[b]Values in parenthesis are standard error of mean.

[c]Means within columns with no common letter(s) are significantly different according to Fisher's Protected LSD test at $P \leq 0.05$.

[d]Growth index = $\pi \times (w/2)^2 \times h$; where *w* is the plant girth calculated as an average of two girths, one measured at the widest point and another perpendicular to the first; and *h* is the plant height.

vigorously and compete with corn/soybean. In such situations, it is important to control giant ragweed early in the season and save soil moisture for the crops. At ≥50% of field capacity, plants were taller (>125 cm) compared with ≤25% field capacity (<70 cm) (Fig. 1*a*). Plant height decreased to 69 and 32 cm at 25% and 12.5% field capacity, respectively, compared with the maximum height (140 cm) achieved at 75% of field capacity. Similar results were obtained by Chauhan and Johnson (2010) in junglerice response to water stress, where maximum and minimum height were recorded at 75% and 12.5% of field capacity, respectively. Number of leaves per plant followed a similar sigmoidal trend (Fig. 1*b*; Table 1). Compared with 100% field capacity (57 leaves plant^{-1}), the number of leaves decreased to 16 and 7 leaves plant^{-1} at 25% and 12.5% of field capacity, respectively (Table 1). In contrast to our results, Chauhan (2013) reported a higher number of leaves in itchgrass at 75% field capacity compared with 100%.

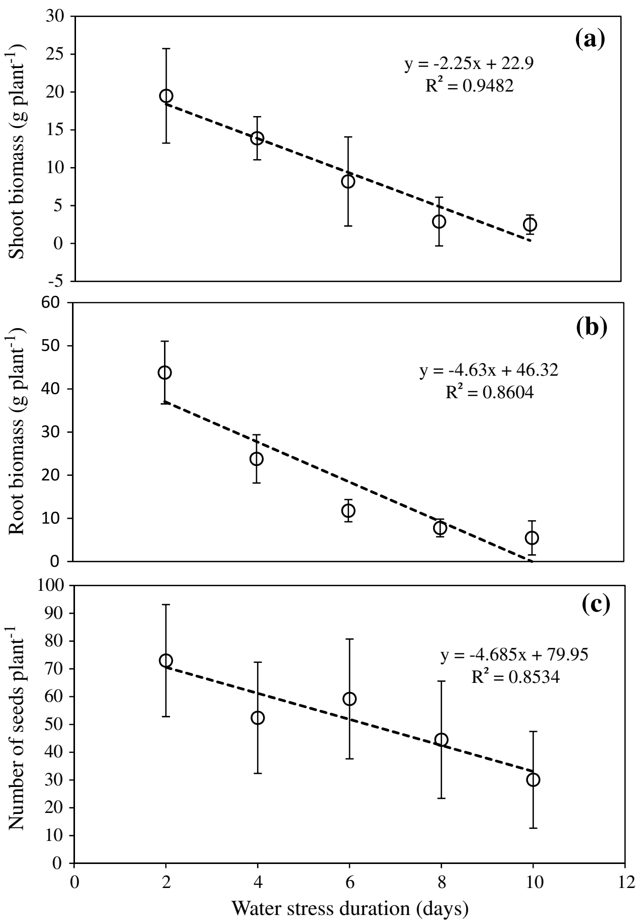
Growth index followed a decreasing trend as percent field capacity decreased (Fig. 1*c*). At <50% of field capacity, growth index decreased to ≤128 cm^3 compared with a maximum of 588 cm^3 at 75% of field capacity. Shoot biomass was 2.1 g plant^{-1} at 12.5% of field capacity compared with 21 g plant^{-1} at 100% field capacity (Figs. 2*a*, 2*b*). Similarly, Chauhan (2013) reported no difference in shoot biomass of itchgrass at ≥50% field capacity; however, there was 81% reduction in shoot biomass at 12.5% field capacity. Root biomass was affected by degree of water stress as evidenced by a 46%–96% reduction at <50% field capacity compared to 59 g plant^{-1} at 100% field capacity (Fig. 2*b*).

The degree of water stress treatments affected giant ragweed seed production (Table 1; Fig. 1*c*). Giant ragweed plants produced ≥60 seeds plant^{-1} at ≥75% field capacity compared to ≤40 seeds plant^{-1} at ≤50% of field capacity (Fig. 2*c*). This relatively small amount of seeds produced per plant even in ≤50% of field capacity may be enough to cause heavy infestation of giant ragweed in the next growing season. Chauhan and Johnson (2010) reported 1680 seeds plant^{-1} at 12.5% of field capacity compared with 100% of field capacity. In a 2 yr giant ragweed emergence study in Nebraska, a 3-fold reduction in giant ragweed emergence was observed in the second year due to the effect of drought in the first year that resulted in a lower number of seeds produced and eventually a reduction in emergence in the second year (Werle et al. 2013).

Duration of water stress

A sigmoidal response of plant height, number of leaves, and seed number was further observed due to varying durations of water stress treatments. Maximum plant height (152 cm) occurred at 4 d of water stress compared with 2 d of water stress (127 cm) (Fig. 3*a*; Table 2). This might be due to water stagnation and aeration problems that may have reduced plant height at 2 d of water stress. It was estimated that 6, 8, and 10 d of water stress resulted in a 33%, 36%, and 51% reduction in plant height, respectively, compared with maximum plant height (152 cm) recorded at 4 d of water stress. Number of leaves per plant decreased as the duration of water stress was prolonged (Fig. 3*b*). The greatest number of leaves (44 leaves plant^{-1}) occurred at 2 d of water stress compared with ≥6 d of water stress (<29 leaves plant^{-1}) (Table 2). Giant ragweed growth index was the highest (529 cm^3) at 2 d of water stress compared with ≥4 d (≤390 cm^3) (Table 2; Fig. 3*c*). Overall results suggested that 2 d of water stress was favorable for the growth and development of giant ragweed; however, plants

Fig. 4. Effect of duration of water stress on giant ragweed (*a*) shoot biomass, (*b*) root biomass, and (*c*) seed production at 18 WAT in a greenhouse study conducted at the University of Nebraska–Lincoln. The vertical bars represent standard error of means (n = 10). Abbreviation: WAT, week after transplanting. The data were regressed using linear model as: Y = $a + bx$, where Y is shoot or root dry biomass or number of seeds plant^{-1}, a is the intercept, b is the slope of the curve, and x is water stress duration (days).



were able to survive at 10 d of water stress. This indicates the ability of giant ragweed plants to survive even if 100% field capacity of water is available at 10 d intervals.

Shoot and root biomass of giant ragweed were affected by varying durations of water stress treatments. For example, shoot biomass was similar (14–18 g plant^{-1}) under 2 and 4 d of water stress treatments, but reduced by 66%–83% at 6 to 10 d of water stress compared with 2 d of water stress (Fig. 4*a*). The highest root biomass (44 g plant^{-1}) was produced at the 2 d of water stress treatment (Fig. 4*b*), most likely because sufficient available moisture might have provided enough opportunity for plants to develop a root system. Water stress for 4 d or longer reduced root biomass (≤24 g plant^{-1}) compared with the 2 d of water stress. In contrast, Chauhan (2013) reported that water stress for 1 and 6 d produced similar root biomass in itchgrass; however, up to a 71% decrease was observed at 12 d of water stress. There was a large variation in the number of seeds produced in response to varying durations of water stress treatments. Seed production was similar at 4, 6, and 8 d of water stress, whereas a difference was observed between 2 and 10 d of water stress (Fig. 4*c*). At 10 d of water stress, plants survived and produced an average of 30 seeds plant^{-1}. This is an important finding because giant ragweed is a riparian weed, but has the capacity to produce seeds even after the 10 d of water stress maintained throughout the study.

Results from this study indicated that giant ragweed attained maximum plant height, number of leaves, seed number, shoot and root biomass, and growth index usually at a soil moisture ≥75% of field capacity or ≤4 d of water stress. At 50% of field capacity, there was no reduction in the growth parameters and number of seeds per plant. Giant ragweed is more sensitive to degree compared with the duration of water stress because at 12.5% of field capacity, few plants were able to survive, whereas at 10 d of water stress, all the plants survived and produced seeds. Nevertheless, moisture levels below 50% of field capacity or water stress for >4 d can decrease giant ragweed growth and seed production potential, but will also result in crop yield loss, mainly due to reduced crop growth and increased crop-weed competition (Geddes et al. 1979; Scott and Geddes 1979). Previous studies have shown that giant ragweed is a highly competitive weed, and 1 to 2 plants m^{-1} can result in significant crop yield losses (Baysinger and Sims 1991; Harrison et al. 2001; Barnett and Steckel 2013).

Results from this study demonstrated considerable reduction in giant ragweed growth and seed production at sub-optimal field capacities (<50%) or longer periods of water stress (>4 d). However, since both corn and soybean require soil moisture to be above 50% of field capacity to avoid yield reduction (Kranz et al. 2008; Kranz and Sprecht 2012), growers will implement favorable soil moisture regimes throughout the growing season in irrigated corn and soybean fields in the Midwest. If giant ragweed plants are not controlled, eventually they will optimally grow, reproduce, and interfere with crops due to the available soil moisture, since giant ragweed plants survived and produced seeds even at 12.5% of field capacity or 10 d of water stress. Giant ragweed is considered a riparian weed; however, it is well established throughout the Midwestern United State in riparian and upland edge habitats. The results of this study indicate that giant ragweed has the ability to survive and produce seeds under extreme water stress conditions, as well as indicating the adaptation of the species to upland habitats. Future research should focus on exploring other cultural and chemical control methods to enhance the competitiveness of corn and soybean to giant ragweed under favorable moisture conditions.

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