

Response of Giant Ragweed (*Ambrosia trifida*) Source Populations to Varying Soil Moisture Conditions

Undergraduate Research Thesis

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By

Kristen Brown

The Ohio State University

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Project Advisors:

Dr. Steve Hovick, Department of Evolution, Ecology, and Organismal Biology

Dr. Matt Davies, School of Environment and Natural Resources

Abstract

Giant ragweed (*Ambrosia trifida*) is native to North America and an emerging invasive species in Europe and Asia. Giant ragweed is typically found in riparian areas, which are located near water sources and have relatively high soil moisture. Giant ragweed often escapes into agricultural fields where it is highly competitive with corn and soybean crops and the soil is much drier. Such incursions into crop fields have been occurring for much longer in the eastern part of the U.S. Corn Belt than in the western Corn Belt, which has led to evolved population differences in the east that are more pronounced than in the west. We hypothesized that giant ragweed populations would differ in drought tolerance due to variable abiotic conditions where they occur. Specifically, we predicted that populations of giant ragweed from crop fields would be more drought tolerant than non-crop populations and that populations from the drier western region would be more drought tolerant than populations from the east. We sourced seeds from agricultural and riparian populations in Ohio and Nebraska. In a greenhouse, we grew each population type and source under three conditions that spanned a soil moisture gradient, from saturated to dry soil moisture conditions. Performance was greatest in the driest conditions for all source populations, with higher germination percentages, higher total biomass, and earlier emergence than in either of the wetter treatments. However, Nebraska populations had a much higher germination percentage and emerged earlier than Ohio populations, which was exacerbated in drier conditions. Additionally, crop populations showed higher germination percentages than non-crop populations, especially in the driest conditions (habitat x treatment). These findings suggest that Nebraska and crop populations may be more drought tolerant than Ohio and non-crop populations, respectively. Overall, giant ragweed is more successful in areas with lower soil moisture content, such as agricultural fields, in comparison to areas with saturated soils. Furthermore, soil moisture similarly affects giant ragweed from varying population types and seed sources. The germination data suggests that there have been adaptive changes in crop populations of giant ragweed

in response to soil moisture. This indicates that adaptive changes across the range of giant ragweed may be more extensive than previously thought.

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Introduction

Giant ragweed (*Ambrosia trifida*) is a floodplain species native to North America. It thrives in disturbed, moist soils such as open stream banks, drainage ditches, and cultivated fields where it outcompetes other plants (Bassett & Crompton, 1982). It is considered a noxious weed that is a significant contributor to seasonal allergies and is detrimental to the agriculture industry (Bassett & Crompton, 1982). It is one of the most competitive annual weeds in soybean, corn, and cotton fields in the U.S. and results in over 50% yield loss in corn and over 75% yield loss in soybean and cotton (Regnier et al., 2016).

Giant ragweed often colonizes a variety of non-riparian edge habitats such as areas around fences and railroads. These edge habitats serve as a network covering most of the U.S. Corn Belt and may act as a corridor for giant ragweed to spread across the landscape. Burrowing earthworms add to the giant ragweed seedbank by collecting and burying large seeds in their burrows, which reduces the likelihood of seed predation and may contribute to the establishment of giant ragweed in crop fields (Regnier et al., 2016).

In non-crop habitats, giant ragweed seedlings tend to emerge earlier and plants grow larger in comparison to other species (Abul-Faith & Bazzaz, 1979; Hovick et al., 2018; Schutte et al., 2012). Giant ragweed grows rapidly and has unusually high photosynthetic rates that allow it to outcompete surrounding species (Abul-Faith & Bazzaz, 1979). These characteristics are likely due to strong selection for strong competitors in a highly dense habitat (Hovick et al., 2018). However, in crop habitats, giant ragweed shows prolonged seedling emergence with seedlings emerging through July (Schutte et al., 2008, 2012). This prolonged emergence is distinct from the early emergence of giant ragweed populations found in environments characterized by infrequent disturbance, such as successional environments and crop fields where giant ragweed is not considered a large threat to agriculture

(Schutte et al., 2012). These differences in seedling emergence are likely in response to strong selection pressure for seedlings that emerge later and avoid early herbicide applications and are thought to indicate genetic differences between giant ragweed populations from different environments (Hovick et al., 2018; Schutte et al., 2012). Non-crop population plants also grow taller, produce more biomass, and have smaller individual fruit mass than crop population plants (Hovick et al., 2018). If we see evolved changes in crop versus non-crop populations in seedling emergence due to these different strong selective pressures, we might also expect differences in drought tolerance, since it is expected that crop fields are drier than the riparian areas that giant ragweed comes from originally.

In addition to expanding its range from non-crop to crop areas, giant ragweed has been expanding westward as an agricultural weed. Although it has been present as a native plant in non-crop areas of the western U.S. Corn Belt, this expansion as an agricultural weed has been suggested to be due to repeated evolution of weediness from local source populations (Li et al., 2022). Differences can be seen between populations from the eastern and western U.S. Corn Belt. Western populations are more fecund, have higher reproductive allocation, and smaller individual fruit mass than eastern populations (Hovick et al., 2018). Seedlings from the western U.S. Corn Belt emerged in a rapid flush during early April while seedlings from the eastern U.S. Corn Belt emerged in a more gradual flush that continued through July (Schutte et al., 2008). The western U.S. Corn Belt is drier and warmer than the eastern U.S. Corn Belt. Given the differences in giant ragweed populations between the eastern and western U.S. Corn Belt and the differences in climate, we might expect to see a greater drought resistance in western populations in comparison to eastern populations. Giant ragweed has developed herbicide resistance and is a genetically variable species capable of rapid evolution in response to herbicide selection pressure. Issues concerning giant ragweed management and herbicide resistant populations have been occurring in a westward trajectory from the eastern U.S. Corn Belt (Regnier et al., 2016).

Giant ragweed shows some flooding-adaptive characteristics. In flooded conditions, giant ragweed invests more biomass aboveground, which indicates phenotypic plasticity. Giant ragweed can also develop adventitious roots, which is common among highly adaptive wetland species (Park et al., 2020). However, giant ragweed struggles to survive in high marsh areas because the high soil moisture is unfavorable for seed survival and growth of seedlings. It is unable to compete as seen in floodplain and agricultural areas because other species are much more tolerant of the waterlogged soils found in high marshes (Sickels & Simpson, 1985).

For this study, we used a common garden experiment to test the hypothesis that giant ragweed is locally adapted to variation in the soil moisture conditions at regional and local spatial scales. We predict that crop populations of giant ragweed will be more drought tolerant than non-crop populations and western populations will show greater drought tolerance than eastern populations. We quantify the variation in traits of Ohio and Nebraska sourced plants and among crop and non-crop population types in response to a soil moisture gradient. We quantify several traits that are common indicators of plant success and weediness including germination percentage, emergence timing, survival, and biomass.

Methods

Set-Up

Giant ragweed seeds were selected from Ohio and Nebraska non-crop and crop populations. Seeds were taken from a total of 59 maternal plants. Seeds from 15 different maternal plants were used for each biotype (crop versus non-crop) and state combination, except for Nebraska's crop population which only had 14 plants. Maternal plants were from one of five populations chosen for this experiment, one crop and one non-crop from Nebraska and one crop and two non-crop from Ohio. Ohio non-crop populations produced fewer seeds, thus it was necessary to take seeds from two different populations to obtain the same amount of replication. All the seeds were stratified at 4°C for six weeks in moist sand before planting. Ten seeds from each maternal plant were planted in an 8-inch or 6-inch sized pots. This was done three times for each maternal plant so that all three soil moisture treatments were represented. Each pot was randomly assigned to one of the treatment groups and the 177 pots were arranged randomly throughout our room in the greenhouse.

A soil moisture gradient was implemented across the three treatments: dry, intermediate, and wet. The dry treatment pots were placed in 12-inch pots with holes and were only watered when the top of the soil had gone dry. The intermediate treatment pots were placed in 12-inch pots with no holes and were intermittently flooded. This was done by filling the 12-inch pot a third of the way full and allowing to completely dry before being filled again. The wet treatment mimicked a riparian area where the plants are constantly water stressed. These pots were placed in 12-inch pots with no holes and soil was never allowed to go dry.

Data Collection

The pots were monitored daily for emergence and watered as described above. After the experiment had started, it was discovered that cockroaches were eating the plants and caused some

seedling mortality. However, the cockroaches did not seem to be targeting a particular population or treatment. The experiment was run from April 26, 2022 to August 1, 2022 and the greenhouse temperature averaged around 29°C. Soil moisture data was taken as percent volumetric water content (vmc%) for each pot after 27 days using a FieldScout TDR 150 Soil Moisture Meter (Spectrum Technologies, Inc., Aurora, Illinois). Randomized thinning began 23 days after emergence and continued until 43 days after emergence so that only one plant remained in each pot. The number of seeds that emerged was recorded before thinning. It was discovered that some of the plants were experiencing nutrient deficiencies, so fertilizer was added to all the pots 48 days after planting.

The giant ragweed plants grew until about half of them had developed inflorescence, which was 93 days after planting. At this point, all the 12-inch pots were removed and watering ceased so that the soil could dry out. Once all soil was dry, aboveground biomass was collected, dried at 60°C for at least 72 hours, and weighed. The soil was then washed from the roots so that belowground biomass could be similarly collected, dried, and weighed.

Data Analysis

All analyses were performed using R Statistical Software (v4.1.1; R Core Team, 2021). General linear mixed models were run in R using the lme4 package (v1.1-30; Bates et al., 2015). The responses of interest included source habitat type, treatment, and state. The full models were response interests as a function of source habitat type, treatment, state, and all two-way and three-way interactions, where all interactions were run as fixed effects. For soil moisture, emergence timing, and germination percent, we also included maternal plant identify nested within its source population as a random effect in all models to account for the non-independence of those maternal plants coming from the same sources. For all other responses, we got error warnings or insufficient sample size with the random effect, so it was dropped. We used general linear models with lme4 with the exception of survival, which used a

generalized linear model with a binomial distribution. Models were simplified with the drop1 command, and inferences about model simplification were based on likelihood ratio tests and AIC. P-values were based on type-3 sums of squares extracted using the package car (v3.1-0; Fox and Weisberg, 2019). Unless otherwise indicated, we present error as 95% CI.

Results

Soil Moisture

There were differences in soil moisture between all treatments, showing that the manipulations were effective (treatment Tukey $p < 0.001$, habitat and state Tukey not significant). The average soil moisture of the dry treatment was 20.4 ± 0.74 (SEM) vwc% (95% CI = 18.95-21.85). The average soil moisture of the intermediate treatment was 57.5 ± 0.75 vwc% (95% CI = 56.04-58.96). The average soil moisture of the wet treatment was 64.8 ± 0.75 vwc% (95% CI = 63.32-66.28).

Germination Percent

Germination percentage varied between habitats (habitat $p = 0.011$; Table 1). Giant ragweed non-crop populations had a 20.5% lower germination percentage than crop populations. Crop and non-crop population germination percentages responded differently to varying soil moisture levels (habitat x treatment $p = 0.023$; Table 1). Crop populations in the wet treatment had an 80% reduction in germination percentage compared to crop populations in the dry treatment (Figure 1B; Tukey $p < 0.001$). Crop populations in the intermediate treatment had a 40% reduction in germination percentage compared to crop populations in the dry treatment (Figure 1B; Tukey $p = 0.003$). Crop populations in the wet treatment had a 67% reduction in germination percentage compared to crop populations in the intermediate treatment (Figure 1B; Tukey $p = 0.006$). Non-crop populations in the wet treatment had a 70% reduction in germination percentage compared to non-crop populations in the dry treatment (Figure 1B; Tukey $p = 0.006$). Non-crop populations in the wet treatment had a 68% reduction in germination percentage compared to non-crop populations in the intermediate treatment (Figure 1B; Tukey $p = 0.003$). However, there is no significant difference between non-crop populations in the intermediate treatment and non-crop populations in the dry treatment (Tukey $p = 0.999$).

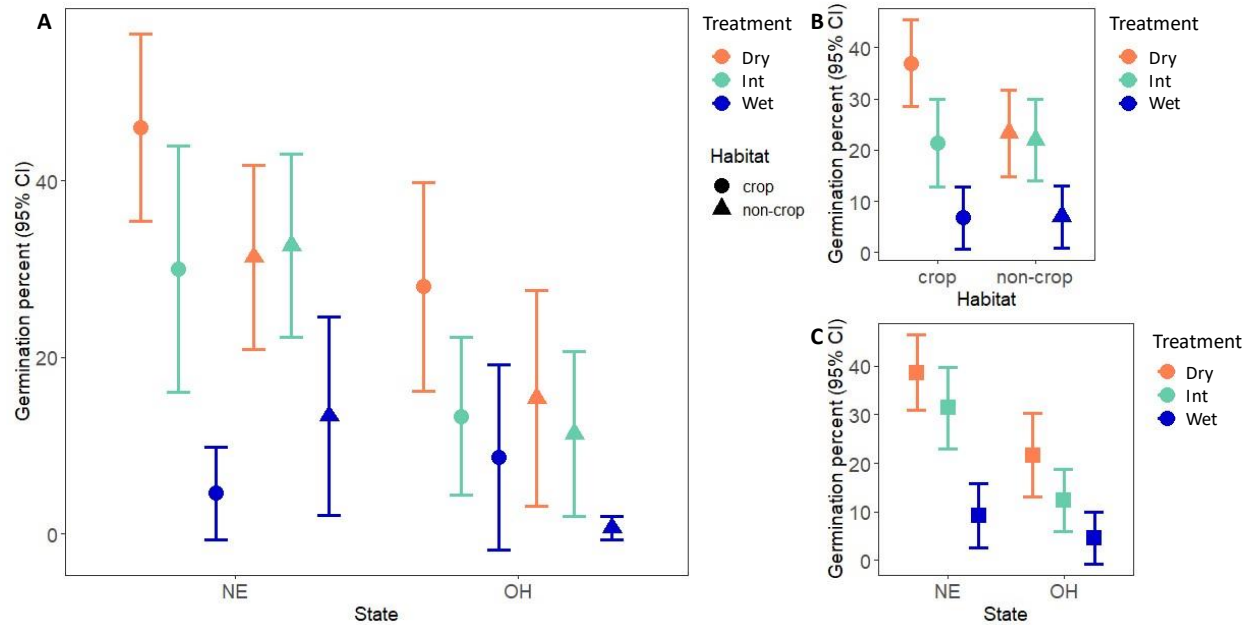


Figure 1. Germination percentage plots. (A) Germination percentages for both habitats and both states in response to the treatments. (B) A subset of 1A, showing the different germination percentages of crop and non-crop populations in response to varying soil moisture levels. (C) A subset of 1A, showing the different germination percentages of Ohio and Nebraska populations in response to varying soil moisture levels.

Germination percentage was higher in Nebraska than Ohio plants on average (state $p=0.002$; Table 1), but the germination rate response to treatment also varied by state of origin. Plants from Ohio and Nebraska differed in their germination response to varying soil moisture levels (Figure 1C; treatment \times state $p<0.029$). Ohio populations in the wet treatment had a 78% reduction in germination percentage compared to Ohio populations in the dry treatment (Figure 1C; Tukey $p<0.001$). Nebraska populations in the wet treatment had a 75% reduction in germination percentage compared to Nebraska populations in the dry treatment (Figure 1C; Tukey $p<0.001$). Nebraska populations in the wet treatment had a 70% reduction in germination percentage compared to Nebraska populations in the intermediate treatment (Figure 1C; Tukey $p<0.001$). Ohio populations in the dry treatment had a 44% reduction in germination percentage compared to Nebraska populations in the dry treatment (Figure 1C; Tukey $p=0.019$). In addition, Ohio populations in the intermediate treatment had a 61% reduction in germination percentage compared to Nebraska populations in the intermediate treatment (Figure 1C;

Tukey $p=0.005$). However, there is no significant difference between Nebraska populations in the wet treatment and Ohio populations in the wet treatment (Figure 1C; Tukey $p=0.939$).

Table 1. Anova p-values for germination percentage, emergence timing, and survival.

Response	Source	F	Df	Pr(>F)
Germination %	Intercept	98.87	1	<0.001
	Habitat	6.70	1	0.011
	Treatment	25.64	2	<0.001
	State	10.43	1	0.002
	Habitat:Treatment	3.91	2	0.023
	Treatment:State	3.66	2	0.029
Emergence Timing	Intercept	23.49	1	<0.001
	Habitat	1.11	1	0.298
	Treatment	4.58	2	0.014
	State	7.59	1	0.009
Survival	Habitat	3.19	1	0.078
	Treatment	3.13	2	0.049
	State	0.73	1	0.396

Emergence Timing

Emergence timing varied between treatments (treatment $p=0.014$; Table 1). Plants in the dry treatment emerged 5-6 days earlier than those in the wet treatment (Figure 2; Tukey $p=0.013$), with the intermediate soil moisture treatment not differing from either of the other treatments (all Tukey $p>0.17$). Emergence timing also varied between states (state; $p=0.009$; Table 1). Nebraska populations emerged about 4 days earlier than Ohio populations (Figure 2; Tukey $p=0.009$).

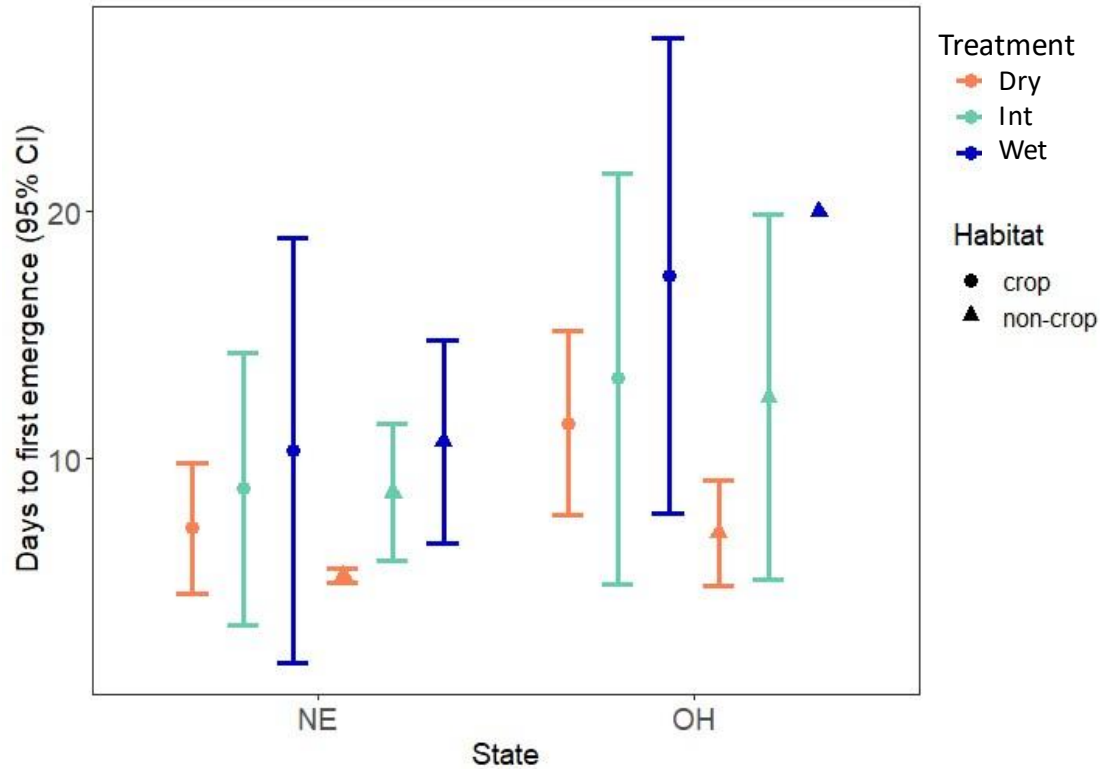


Figure 2. Variation in emergence timing of both habitats and both states in response to varying soil moisture levels.

Survival

Survival varied between treatments (treatment $p=0.049$; Table 1). Plants in the wet treatment had a 69% reduction in survival compared to plants in the dry treatment (Tukey $p=0.045$). The survival of dry treatment plants was 66.7% and the survival of wet treatment plants was 20.7%. The survival of plants in the intermediate treatment (55.9% survival) was in the middle and not significantly different from the other treatments (both Tukey $p>0.275$). Variation in survival between habitats was marginally significant (habitat $p=0.078$; Table 1). Plants from the crop habitat had a 51.7% lower survival rate than plants from the non-crop habitat. The survival of non-crop plants was 45.6% and the survival of crop plants was 50.6%. The survival of wet treatment seedlings was especially low when broken down by state and habitat combinations. The survival rates in the wet treatment were 46.7%, 15.4%, 6.7%, and 13.3% for Nebraska non-crop, Nebraska crop, Ohio non-crop, and Ohio crop populations respectively.

The survival rate for Nebraska non-crop appears to be higher than 20.7% while the rest of the populations had a survival rate lower than 20.7%.

Biomass

Low survival in our wettest treatment meant that sample sizes were very limited for biomass-based analyses, especially for Ohio non-crop populations, for which we had only one surviving plant. We therefore present a simplified analysis that excludes the wettest treatment (although data from all treatments are still presented in the relevant figures).

The highest aboveground and belowground biomass was seen in plants from the dry treatment group (treatment; all Tukey $p \leq 0.021$).

The difference in aboveground biomass in response to variation in treatment between Ohio and Nebraska populations was found to be marginally significant (treatment x state $p = 0.082$; Table 2). Ohio populations in the intermediate treatment had a 57% reduction in aboveground biomass compared to Ohio populations in the dry treatment (Figure 3A; Tukey $p = 0.004$). Nebraska populations in the intermediate treatment had a 23% reduction in aboveground biomass compared to Nebraska populations in the dry treatment (Figure 3A; Tukey $p = 0.325$). Ohio populations in the intermediate treatment had a 54% reduction in aboveground biomass compared to Nebraska populations in the dry treatment (Figure 3A; Tukey $p = 0.009$). All other state x treatment pairwise comparisons were not different from each other (all remaining Tukey $p > 0.05$). Aboveground biomass did not differ between crop and non-crop populations.

Table 2. Anova p-values for biomass without the wet treatment. Wet treatment was not included in analyses due to small sample size and an outlier that skewed results.

Response	Source	F	Df	Pr(>F)
Aboveground Biomass	Intercept	89.12	1	<0.001
	Treatment	2.93	1	0.091
	State	0.33	1	0.569
	Habitat	0.37	1	0.546
	Treatment:State	3.12	1	0.082
Belowground Biomass	Intercept	149.56	1	<0.001
	Treatment	40.38	1	<0.001
	State	0.20	1	0.658
	Habitat	0.0197	1	0.889
Root Mass Ratio	Intercept	426.63	1	<0.001
	Treatment	26.40	1	<0.001
	State	2.85	1	0.096
	Habitat	6.37	1	0.014
	Habitat:State	6.42	1	0.014

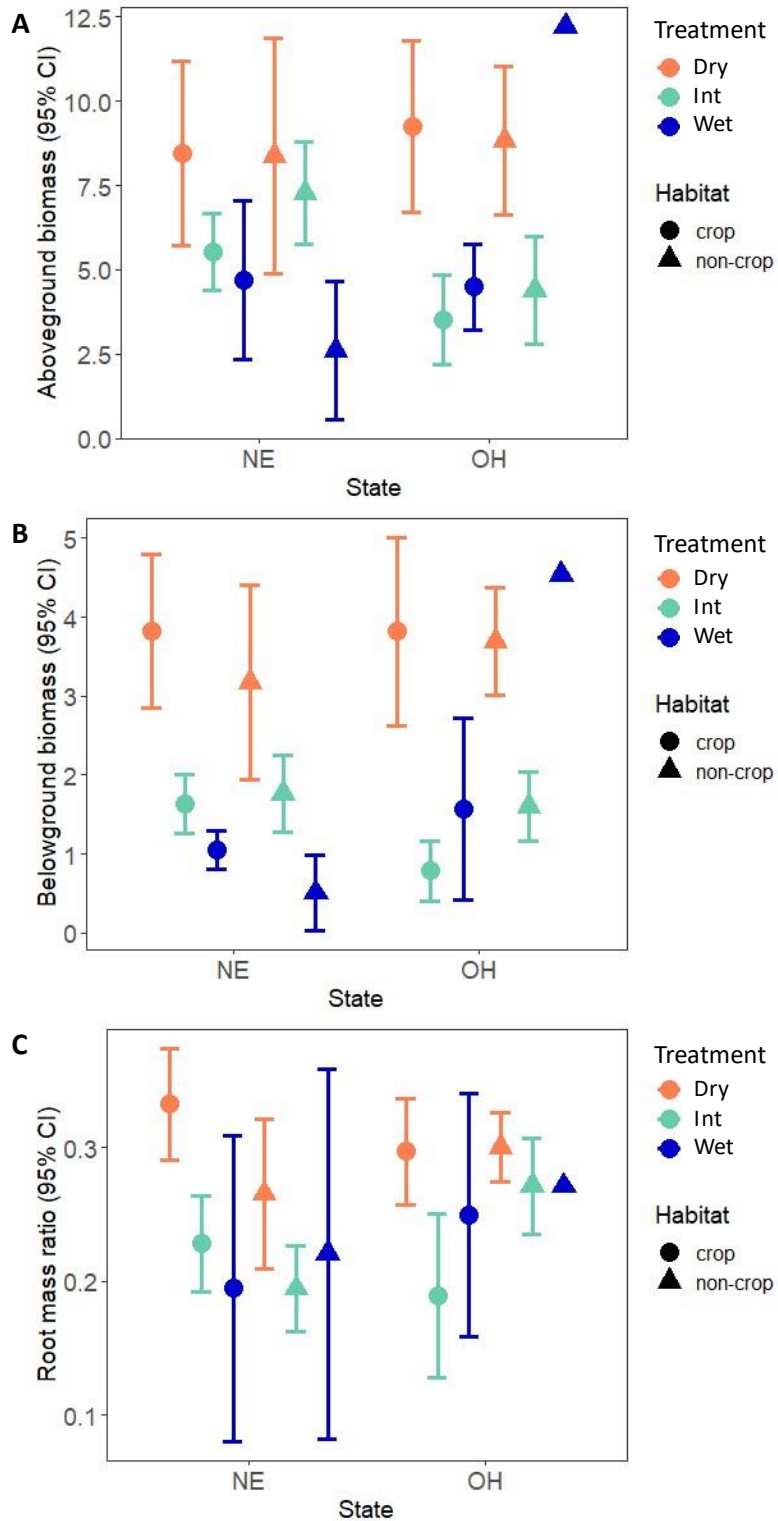


Figure 3. Biomass plots. (A) Variation in aboveground biomass of both habitats and both states in response to varying soil moisture levels. (B) Variation in belowground biomass of both habitats and both states in response to varying soil moisture levels. (C) Variation in root mass ratio of both habitats and both states in response to varying soil moisture levels.

Belowground biomass varied between treatments (treatment $p < 0.001$, Table 2). Intermediate treatment plants had a 59% reduction in belowground biomass compared to dry treatment plants (Figure 3B; Tukey $p < 0.001$). Belowground biomass did not differ between crop and non-crop populations or Ohio and Nebraska populations.

Root mass ratio also varied between treatments (treatment $p < 0.001$, Table 2). Intermediate treatment plants had a 28% reduction in root mass ratio compared to dry treatment plants (Figure 3C; Tukey $p < 0.001$). Root mass ratio varied between habitats (habitat $p = 0.014$, Table 2). The difference in root mass ratio response to variation in habitat between Ohio and Nebraska populations was also found to be significant (habitat \times state; $p = 0.014$; Table 2). Nebraska crop populations had an 18.1% reduction in root mass ratio compared to Nebraska non-crop populations, which was found to be marginally significant (Figure 3C; Tukey $p = 0.065$). The root mass ratios are all very clustered (Figure 3C), resulting in no other significant Tukey results. A likely contributor to the significance of the habitat \times state interaction is the higher root mass ratio in non-crop populations in comparison to crop populations from Ohio, but the opposite pattern is seen in Nebraska with higher root mass ratio in crop populations. Ohio crop populations (mean=0.245) had a 12.5% reduction in root mass ratio compared to Ohio non-crop populations (mean=0.280). Nebraska non-crop populations (mean=0.231) had an 18.1% reduction in root mass ratio compared to Nebraska crop populations (mean=0.282).

Discussion

It was found that giant ragweed performance was generally better in drier conditions and poorer in saturated conditions. Germination percentage, survival, aboveground biomass, and belowground biomass decreased with increasing soil moisture. These results are similar to previous findings that found while giant ragweed can survive in a wide range of soil moisture conditions, the highest germination is seen at 20-33% soil moisture, which is similar to our dry treatment conditions (Abul-Faith & Bazzaz, 1979). Even though giant ragweed is considered a riparian species, it does not prefer saturated soils and thus is presumably stressed to some extent in these more saturated conditions.

Germination Percent

Germination percentages decreased with increasing soil moisture for both Ohio and Nebraska populations. However, Nebraska populations had higher germination percentages than Ohio populations. The dry and intermediate treatments for Nebraska had much higher germination percentages than Nebraska wet and all the Ohio treatments. Since Nebraska gets less precipitation and is usually warmer than Ohio, this pattern may be because Nebraska populations are better adapted to drier conditions than Ohio populations. These results are similar to the findings of a common garden study done with Douglas-fir (Bansal et al., 2014). Populations originating from warm and dry sites were found to be more drought-resistant than populations from moderate or cool and moist sites. It was also suggested that populations from regions with cool winters and arid summers may be the most drought adapted. Douglas-fir trees growing in cooler climates are better adapted to harsh winter conditions which have been linked to increased transpiration and drought-induced mortality. By protecting themselves against winter-desiccation, these trees have evolved mechanisms to increase drought resistance (Bansal et al., 2014). Nebraska tends to have colder winters than Ohio, which may also contribute to drought stress and therefore drought tolerance in Nebraska populations.

Germination percentages decreased with increasing soil moisture for both crop and non-crop populations. The dry treatment for crop populations was much higher than the dry treatment for non-crop populations, however the intermediate and wet treatments had similar germination percentages for both crop and non-crop. Crop populations may be more adapted to dry conditions than non-crop populations. This adaptation requires that there is little gene flow between crop and non-crop populations or if gene flow is present, then there must be strong selection pressures that increase germination in crop populations.

Emergence Timing

Nebraska populations emerged earlier than Ohio populations, which has been seen in previous studies (Schutte et al., 2008). A possible explanation for this observation is that Ohio populations have had more time to evolve this later emergence in order to survive in crop habitats. Similarly, Nebraska populations in agricultural settings may be more phenotypically similar to non-crop populations in having uniformly rapid emergence because the crop and non-crop populations have not diverged evolutionarily.

We found that emergence timing was more rapid in drier soils. A study done with Mediterranean oak species found that high soil moisture levels lengthened the emergence timing of seedlings, meaning that emergence timing was more rapid in drier soils (Urbieta et al., 2008). The extended time that giant ragweed takes to emerge under high soil moisture conditions may be a stress response to an over-abundance of water. The lack of difference in emergence timing based on habitat contrasts with what has been previously shown in Ohio populations where non-crop populations emerge earlier than crop populations (Schutte et al., 2012). However, the emergence timing pattern in Schutte et al. (2012) was only reported for naturally overwintering seeds, not induced cold stratification such as our experiment. This leaves the question, are timing differences influenced by the way

dormancy is broken? Or perhaps early emergence is a stress response to dry soil conditions that overrides the adaptation of crop populations that allows them to emerge later.

Biomass

It was found that aboveground biomass decreased as soil moisture increased for both Ohio and Nebraska populations. While the state x treatment interaction is only marginally significant, Ohio and Nebraska populations in the intermediate treatment had a 57% and 23% reduction in aboveground biomass compared to populations in the dry treatment respectively. These results contrast with belowground biomass, where the decrease from dry to intermediate appears to be the same and there is no hint of an interaction between state and treatment. This also contrasts with germination patterns since the separation between Nebraska and Ohio populations is seen in the wetter conditions and not the drier conditions. In other words, there is a maximum biomass in dry conditions, regardless of state, and as conditions get wetter there is a greater drop in aboveground biomass for Ohio populations and a lesser drop for Nebraska populations. However, for germination, Ohio and Nebraska populations decrease similarly in wet conditions and the difference is magnified in dry conditions. This may indicate that giant ragweed populations from Ohio are more stressed than Nebraska populations, causing them to put on less aboveground biomass, but not so stressed that it impacts belowground biomass and germination.

Similarly to aboveground biomass, belowground biomass decreased as soil moisture increased. Belowground biomass for dry treatments was much higher than the intermediate treatment. These results indicate that giant ragweed prefers drier habitats and tends to get stressed in wetter environments.

Root mass ratio decreased as soil moisture increased. Root mass ratio was slightly higher in dry treatments than in intermediate treatments. This is expected since plants put relatively more

investment into root growth in drier conditions. Root mass ratio also appears to be constitutively higher in Ohio non-crop populations versus crop populations, which is opposite of the Nebraska pattern where crop root mass ratio is higher than non-crop root mass ratio. It appears that the surprisingly high root mass ratio for Ohio non-crop populations is driven by surprisingly high belowground biomass under intermediate soil moisture. Ohio non-crop grown in the intermediate treatment has less of a decrease than other populations grown in the intermediate treatment would suggest.

Conclusion

Overall, we found that giant ragweed performs better in lower soil moisture conditions, regardless of population. Our findings suggest that Nebraska and crop populations may be more drought tolerant than Ohio and non-crop populations, respectively. The earlier emergence we observed in all Nebraska populations suggests that those populations may not yet have had enough time to evolve a difference between crop and non-crop populations and we may not see the delayed emergence in crop populations that is seen in Ohio. Additionally, the stress from constant flooding results in later emergence across all populations. More research is needed to determine if the way dormancy is broken impacts emergence timing in giant ragweed.

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