

THE IMPACT OF ALTERED PRECIPITATION VARIABILITY ON ANNUAL WEED SPECIES¹

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- **Premise of the study:** Climate change models predict increasing variability in precipitation across the globe, with an increase in the incidence of large precipitation events but decreasing overall event frequency. Research with annual species in arid and semiarid ecosystems has demonstrated that precipitation variability can influence plant community dynamics; however, less is known about the impact of precipitation variability in less water-limited ecosystems, including economically important agricultural systems.
- **Methods:** We conducted three greenhouse experiments to determine how variation in total precipitation and the interval between precipitation events affected emergence and growth of two common annual midwestern weed species, *Chenopodium album* (Chenopodiaceae) and *Setaria faberi* (Poaceae).
- **Key results:** Both species responded to precipitation variability; however, the effect depended on life stage and precipitation amount, indicating that responses are highly context-dependent. Emergence of both species increased with longer intervals between precipitation events at low total precipitation, but species' responses varied under typical precipitation amounts. Individual seedling biomass of both species depended on interactions between total water and interval, but species' responses differed; *Setaria faberi* biomass was reduced with longer intervals, but *Chenopodium album* had either a positive or no response.
- **Conclusions:** Our results suggest that changes in precipitation variability likely will affect the composition and relative abundance of agriculturally important weeds. These results are important for understanding how changes in the temporal variability of precipitation due to global climate changes could impact plants in non-arid communities.

Key words: annual weeds; Chenopodiaceae; *Chenopodium album*; climate change; Poaceae; precipitation variability; *Setaria faberi*.

Water availability affects plant community productivity (Laurenroth and Sala, 1992; Knapp and Smith, 2001; Suttle et al., 2007) and species composition (Silvertown et al., 1999). Climate change models predict increasing variability in precipitation across the globe—both in annual amount and in temporal distribution, with less frequent, larger precipitation events expected to increase (Easterling et al., 2000; Weltzin et al., 2003; IPCC, 2007). Previous research has shown that precipitation variability plays an important role in structuring annual plant communities in arid and semiarid ecosystems (Pake and Venable, 1995, 1996; Clauss and Venable, 2000; Schwinning and Sala, 2004; Sher et al., 2004). However, less is known about how increased variability in precipitation will affect plant communities in less water-limited ecosystems (but see Knapp et al., 2002 and Fay et al., 2008). In addition, species in less water-limited systems may respond differently to variability in precipitation delivery than arid systems, for example, with variability increasing growth in arid ecosystems and decreasing it in less water-limited systems. (Knapp et al., 2008; Heisler-White et al., 2009).

Understanding how plant species respond to altered precipitation regimes will be important for predicting shifts in plant communities and managing pest species and species of conservation interest.

Annual plant communities are likely to be strongly responsive to altered precipitation regimes because species composition and abundance are driven by germination dynamics that often depend on water availability (Baskin and Baskin, 1998; Lundholm and Larson, 2004). Events early in the growing season can have long-lasting impacts in annual communities (Ross and Harper, 1972; Levine et al., 2008). Variation in water availability throughout the growing season may also directly affect plant growth (Novoplansky and Goldberg, 2001; Sher et al., 2004). Weeds in row crop agriculture provide a widespread and economically important system dominated by annual plants (Davis et al., 2005) to examine the impacts of precipitation variability. In addition, knowledge of how annual weed communities respond to precipitation variability may have important consequences for agricultural management practices.

We conducted three greenhouse experiments to address whether altered precipitation regimes would impact annual weed communities. Specifically we asked: (1) Will changes in precipitation patterns—amount and variability—affect the emergence and relative abundance of weed species? (2) Do species differ in their early growth responses to altered precipitation? Although there are a large number of weed species that occur in midwestern agriculture, we focused on two species, *Setaria faberi* (Poaceae) and *Chenopodium album* (Chenopodiaceae), which are common in row crop agricultural systems in the midwestern United States and dominated our study system (described next).

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MATERIALS AND METHODS

Experimental overview—We conducted three experiments in a temperature-controlled greenhouse with supplemental lighting at the W. K. Kellogg Biological Station (KBS) of Michigan State University between January 2008 and June 2008. All experiments used soil and seeds collected from annually tilled areas of successional plots established at the KBS Long Term Ecological Research (LTER) site in southwest Michigan (http://lter.kbs.msu.edu/about/experimental_design.php). These fields are tilled every spring and are dominated by annual weed species common in row crop agriculture in the region (Davis et al., 2005). We collected surface soil (~0–5 cm) for the experiments from all six replicate plots of this experiment and homogenized the soil by sieving through a 1.5-cm sieve to remove stones and rhizomes. During all three experiments, we rotated the pots on the greenhouse bench every other day to minimize any location effects. We also mimicked late spring/early summer conditions temperatures in southern Michigan by setting the greenhouse temperature to range from a maximum of 29.4°C to a minimum of 15.5°C. The supplemental lighting used depended on the time of year and is described for each experiment.

All experiments used the same 2 × 3 factorial design, with two levels of total water (average and low) and three watering intervals (4, 8, and 12 d between events). The amount of water added to the average water treatment was based on a 10-yr record of growing season precipitation (May–August 1996–2005) at the KBS LTER site. We used the median growing season precipitation (314 mm) over this period to calculate a mean daily precipitation amount for the average treatment and set the low water treatment at 50% of the average amount, in line with predictions from the driest model scenario for the region (Kling et al., 2003). The interval treatments varied the amount of time (interval) between watering events while keeping total water constant, leading to water additions of 10.2 (4-d), 20.4 (8-d), and 30.6 (12-d) mm of water in the average water treatment. All pots were watered by hand with deionized water, with the volume of water adjusted for surface area across experiments. For large volumes of water, we spread the delivery of the water over several hours to prevent pooling and to allow for more natural infiltration. Adding the water over time resulted in virtually no water loss due to drainage from the pots.

Because we were interested in the effects of precipitation variation on germination, we used early season (May) data from the KBS LTER precipitation records to determine current “typical” intervals between precipitation events. From 1996–2005, the longest dry periods in May ranged from 4 to 10 d, with an average of 6 d. The maximum observed interval between rainfall events during the growing season over this period was 15 d. Based on these data, we established interval lengths for the experiment of 4, 8, and 12 d. These intervals are within the range of variation in rainfall currently observed over the entire growing season for this site, though 12-d intervals occur primarily later in the growing season (July and August). Imposing treatments that are at, or just beyond, the current variability is important because predicted climate change models suggest scenarios outside the current natural variation (Nippert et al., 2006).

In the first experiment, we measured the effects of altered precipitation regimes on seedling emergence and early seedling growth for all species that emerged from the soil seedbank. The other two experiments focused on the two most common species that emerged in the first experiment (*Setaria faberi* and *Chenopodium album*) and examined species-specific germination (experiment 2) and individual seedling growth (experiment 3) responses to precipitation variation. We analyzed data from all three experiments using a linear model to test for the effects of total water, interval, and their interaction using the program JMP (version 5, 1989–2007; SAS Institute, Cary, North Carolina, USA). In the third experiment, we included planting date as a covariate. We conducted our final census, or harvest, several days after the last watering event to allow treatments to respond to the final water pulse. Each response variable was checked for deviations from normality, and we used logarithmic and square root transformations as necessary to meet homoscedasticity assumptions. Untransformed data are shown in the figures.

Experiment 1: Emergence from the seedbank and growth—To determine how altered precipitation patterns affected the number and composition of weeds emerging from the seedbank, we followed seedling emergence and growth for almost 2 months after the experiment was initiated. The experiment was established in late January by filling twenty-four 16-cm diameter pots with 20 cm of air-dried soil collected the previous October from the LTER field site. The soil was stored in an unheated garage until the start of the experiment after being homogenized. Homogenizing the soil addressed any variation in soil or seed bank characteristics between replicate sampling areas (Davis et al., 2005). In this experiment, we used supplemental lighting to increase day length to 14.5 h

(0700 to 0930 hours) to simulate conditions in May, when weed seeds would typically germinate in the field following spring tillage. Watering treatments began on 29 January and continued for 48 d until 13 March for a total of 91.8 mm of water added in the average treatment. Every 4 d, we recorded the number of seedlings that emerged, categorizing individuals by life form (monocot or dicot) and species when possible. We ended the experiment on 18 March (53 d after initiation) and harvested the aboveground biomass for each species and oven dried it at 60°C for a minimum of 72 h. Germination data were square-root transformed, and *S. faberi* biomass data were log-transformed to meet assumptions of normality.

Experiment 2: Germination responses of sown seeds—To more precisely determine germination responses of the most common species that emerged in the first experiment (*S. faberi* and *C. album*) to precipitation variability, we conducted an experiment where we used known numbers of seeds of these two species. We collected seeds for this experiment from plants growing in the KBS LTER field site in the fall of 2007. Seeds were stored until May 2008 at alternating temperatures (~7°C and ~17°C) every 2 weeks to mimic freeze–thaw cycles over the winter–spring in SW Michigan. We used autoclaved soil for this experiment to eliminate the seedbank. We placed 5 cm of sterilized soil in 8.5 × 8.5 cm pots, rinsed the soil with water, and then allowed it to air dry to a constant mass. We sowed 50 seeds of each species into separate pots, with six replicates of each treatment combination (36 pots for each species) using the same 2 × 3 factorial design described above. We covered the seeds with a thin layer of soil and then added 1.2 cm of water to each pot as an initial watering. We did not use any supplemental lighting in this experiment because the time of the experiment (late May) coincided with the typical season for seedling emergence for these species.

The experimental watering treatments were initiated on 27 May and continued until 16 June, allowing for two cycles of the longest and six cycles of the shortest interval treatments. A total of 61.2 mm of water was added to all of the pots in the average and 30.6 mm in the low precipitation treatments. We censused and rotated the pots every 2 d until the experiment was terminated (22 June, 30 d after initial watering). We tested for species’ responses to the precipitation treatments using the total number of seeds germinating in a linear model with total water, interval, and their interaction. Data for *C. album* germination were log-transformed to meet assumptions of normality.

Experiment 3: Individual plant biomass—To disentangle the direct effects of altered precipitation and seedling density on species growth, we grew individual *S. faberi* and *C. album* seedlings in pots and monitored their growth in response to the same 2 × 3 factorial watering treatments. Seeds from the same field collection as experiment 2 were germinated in the greenhouse on moistened filter paper in petri dishes. Newly emerged seedlings were transplanted into containers (3.76 cm diameter × 20 cm depth; Stuewe and Sons, Tangent, Oregon, USA) filled with air-dried soil from the field site (collected as described in experiment 1) and topped with 2 cm of autoclaved soil. All seedlings received 10 mL and 15 mL of water on the first and second day, respectively, following transplantation and no additional water until the experimental treatments were initiated on the fourth day after transplantation. Seedlings that died during the first 2 weeks of the experiment were replaced; a total of 48 *S. faberi* (eight replicates) and 36 *C. album* seedlings (six replicates) were grown for 30 d for this experiment. Seedlings in the average water treatment received a total of 61.2 mm of water during the experiment and those in the low treatment 30.6 mm. We harvested and dried aboveground biomass following the protocol used in the experiment 1. We analyzed final biomass with a linear model testing for the effects of total water, interval, and their interaction and used planting date as a covariate. We excluded the 12-d interval for *C. album* from these analyses because seedling mortality was high, particularly in the low water treatment (>60%).

RESULTS

Emergence from the seedbank and growth—In total, over 2000 seedlings emerged in this experiment, and the majority (88%) were monocots. Over 99% of monocot seedlings were *S. faberi*, and this species accounted for a similar proportion of the total biomass in each pot. As a consequence, total community biomass responses mirrored the *S. faberi* responses to precipitation treatments. *Chenopodium album* made up over 98% of

dicot seedlings that emerged and over 95% of dicot biomass. Consequently, we focus on the response of these two species to our experimental watering treatments.

Both total water and the interval between watering events affected emergence from the seedbank, but *S. faberi* and *C. album* responded differently. *Setaria faberi* germination increased with longer intervals in the low water treatment, but interval had no impact on germination at the average moisture treatment (interaction $F_{1,20} = 15.3605$, $P < 0.0001$). In contrast, *C. album* germination increased in response to both higher water amount and longer intervals (total water $F_{1,20} = 116.2825$, $P = 0.0008$ and interval $F_{1,20} = 23.5319$, $P < 0.0001$).

Setaria faberi final biomass decreased with longer intervals under average moisture but increased with longer intervals when moisture was low (interaction $F_{1,20} = 34.5754$, $P < 0.0001$, Fig. 1A), though total biomass was still higher under average moisture (Fig. 1). *Chenopodium album* biomass was greater at average than low water amounts ($F_{1,20} = 28.7816$, $P < 0.0001$, Fig. 1B) but showed no response to interval length.

Germination responses of sown seeds—Overall, germination of *S. faberi* was higher (37.3%) than that of *C. album* (1.3%) in this experiment. Germination of both species showed interactive effects of precipitation amount and interval but differed in how they responded. Germination of *S. faberi* was higher at longer intervals at both levels of total water, though the magnitude of the effect was greater at the low watering treatment (interaction $F_{1,32} = 4.5623$, $P < 0.0404$, Fig. 1C). In contrast, *C. album* germination increased with longer intervals at low water but showed no response to interval at average levels of moisture (interaction $F_{1,32} = 4.9821$, $P < 0.0327$, Fig. 1D).

Individual plant biomass—The biomass of both species when grown individually responded to the interaction of total water and interval but in opposite directions. Individual *S. faberi* biomass decreased with longer intervals at both the average and low watering levels, but the decrease in biomass was greater under average moisture (interaction $F_{1,41} = 4.8739$, $P = 0.0329$, Fig. 1E). Biomass of *C. album* seedlings increased with an increase in interval from 4 to 8 d at average moisture but showed no response to interval length at low levels of moisture (interaction $F_{1,23} = 6.6042$, $P = 0.0171$, Fig. 1F).

DISCUSSION

Precipitation variability affected both germination and growth of two common weed species, *S. faberi* and *C. album*, though not in the same manner. In addition, the magnitude and direction of the effects varied with life stage. Longer intervals between precipitation events consistently increased germination of both species under low, but not average, watering treatments. However, *S. faberi* biomass decreased with longer intervals, while *C. album* biomass either increased or remained unaffected. Previous research has shown a strong relationship between biomass and seed production for both species (Bussan et al., 2000; Grundy et al., 2004), suggesting that increasing precipitation variation may impact the relative fitness of these two species. The pronounced response of both species to interval length suggests that predicted changes in storm frequency and intensity (Easterling et al., 2000; Weltzin et al., 2003; IPCC, 2007) could impact the overall abundance and species compo-

sition of weed communities in row crops, particularly if spring precipitation is reduced.

Increased emergence with longer intervals may result from seeds needing to reach a minimum level of moisture for germination (Baskin and Baskin, 1998). The larger amounts of water available at one time in the longer interval treatments could promote germination rates if these species have to be exposed to a threshold moisture level to germinate. These results are consistent with a study by Bouwmeester (1990) that found *C. album* germination was stimulated by desiccation events. The lack of a consistent response to interval length at average moisture suggests that germination was being determined by factors other than moisture, such as temperature (Leblanc et al., 2002) or light (Baskin and Baskin, 1998). In addition, seed traits such as size may play a role in determining germination responses. While both of the species in our study have relatively small seeds, *C. album* had a smaller average seed mass than *S. faberi* (0.2 mg vs. 1.75 mg). Differences in seed mass between species have been correlated with germination responses to water (Daws et al., 2008), so seed mass, along with other seed traits, may play an important role in determining germination responses to precipitation variability. Altered precipitation regimes may change the relative timing and density of seedling emergence, and there is evidence that *C. album* biomass may increase with earlier germination times (Miller, 1987). However, further work with more species under field conditions could identify whether shifts in initial density, like those we see, lead to shifts in the relative abundance of species at the end of the season. Such work could also incorporate temperature effects predicted due to climate change, which may make water more or less limiting.

How annual weed communities respond to altered precipitation will depend not only on seedling emergence but also growth and competitive interactions among species. Species' differences in root morphology may explain the differences in plant growth responses we observed in these experiments, *C. album* (positive/neutral) and *S. faberi* (negative) to longer intervals when precipitation events are large. *Chenopodium album* has a taproot that may allow it to access water that infiltrates deeper into the soil following large rain events, similar to shrubs. In contrast, *S. faberi* has a fibrous and shallower root system that may limit its ability to access deeper soil water. This could make *S. faberi* more sensitive to variation in surface soil moisture and is consistent with previous work (Dalley et al., 2006) that found evidence of deeper moisture use by *C. album* than *S. faberi* in cornfields. Walter (1971) suggested that shrubs and grasses could partition soil moisture, with deeper rooting shrubs accessing deep water not accessible to grasses, and there is some limited evidence that this can happen (McCarron and Knapp, 2001). It is important to note that *C. album* mortality was high in the individual growth experiment, so this may not be representative of how *C. album* would respond to variation in precipitation in the field. *Setaria faberi* biomass declined in both the individual seedling experiment and community experiment, and only in the community experiment could this response be potentially attributed to increased competition due to higher seedling emergence and density in the pots. Species' differences in root morphology could provide an explanation for the observed differences in growth of these species and, if true, that information could inform weed management practices. We did observe differences in rooting depth and production across treatments when we harvested the plants in the seedbank study that appeared to follow the difference in aboveground biomass

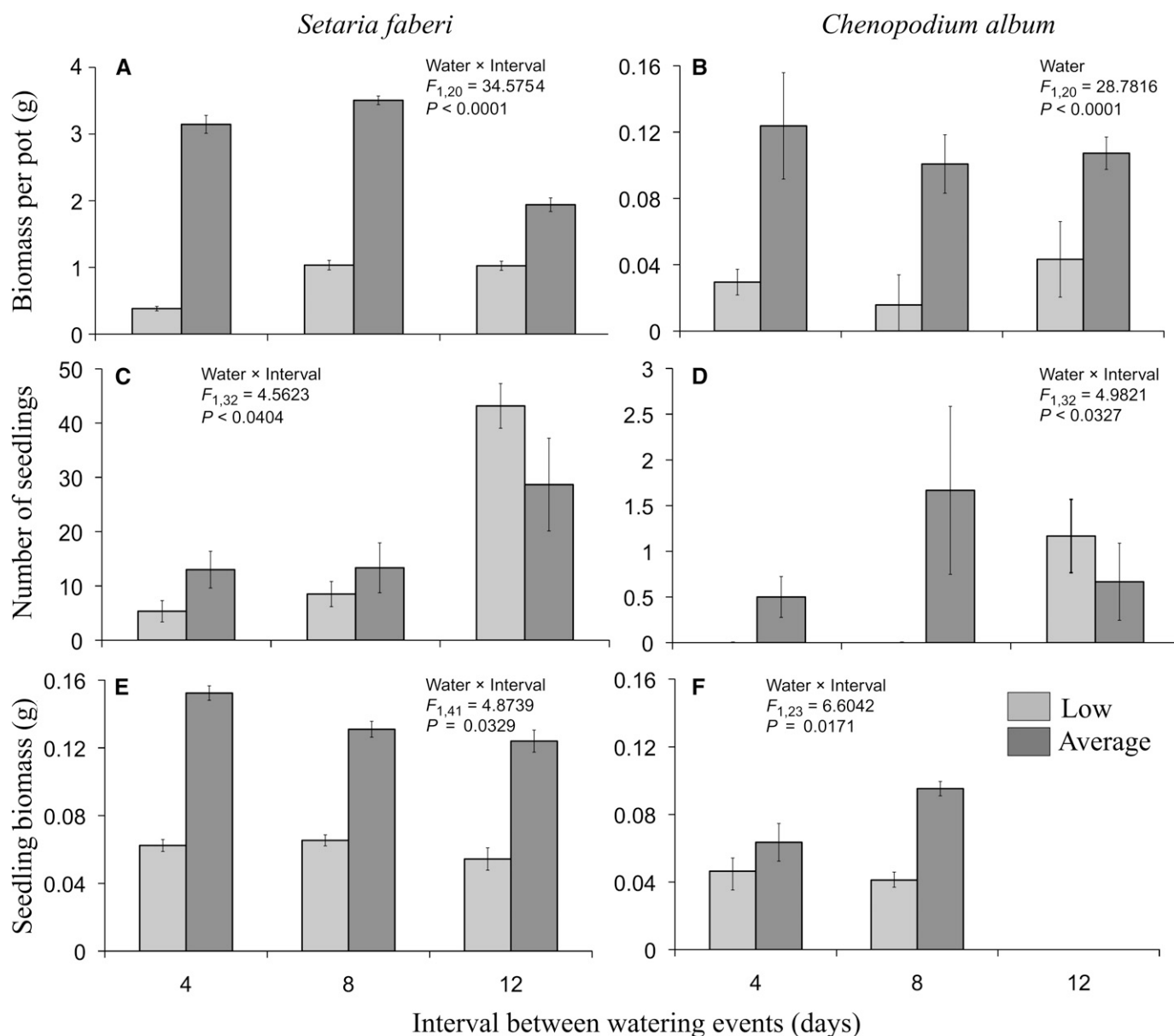


Fig. 1. Biomass and germination responses of *Setaria faberi* and *Chenopodium album* to variation in precipitation amount and interval between watering events in the greenhouse. Total biomass of (A) *S. faberi* and (B) *C. album* from the seedbank emergence experiment. Mean number of seedling emerging of (C) *S. faberi* and (D) *C. album* when known numbers of seeds were sown. Average individual seedling biomass of (E) *S. faberi* and (F) *C. album* when plants were grown individually. Bars are standard errors; N varied by experiment (see text).

in these treatments (T. Robinson, personal observation). We did not harvest roots in this experiment because we could not reliably separate roots by species in the mixed community experiments, so it is not clear if species differed in belowground production or other factors that could impact their responses to precipitation variation. Overall, our results suggest that depending on the balance between reduced growth and enhanced germination, *S. faberi* may become less abundant relative to *C. album* as precipitation becomes more variable, but weed community productivity may be buffered by differences in species' responses.

All these experiments were conducted in the greenhouse, which allowed us to control other environmental variables that can impact seedling emergence and growth. The size of the pots

and scale of the experiment only allowed us to focus on the effects of precipitation variability early in the life cycle of these species. Using small pots for these studies may have introduced some artifacts into the experiments. For example, soil in pots will dry faster than in a continuous soil profile, exacerbating the effects of longer intervals or reduced total water. While the direction and magnitude were context dependent, our results show that precipitation variability could have marked impacts on the emergence and establishment of two species that are common agricultural weeds in the Midwest United States. Further work in the field is needed to determine if the responses observed here occur in the field, to evaluate the impact across the growing season, and any implications for irrigation management.

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