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Author(s): James E. Moore and John D. Wolfe Scott B. Franklin


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Growth responses of different aged individuals of *Xanthium strumarium* L. in flooded conditions

James E. Moore¹ and John D. Wolfe

Department of Biology, Christian Brothers University, Memphis, TN 38104

Scott B. Franklin

Department of Biological Sciences, The University of Northern Colorado, Greeley, CO 80639

MOORE, J. E., J. D. WOLFE (Department of Biology, Christian Brothers University, Memphis, TN 38104), and S. B. FRANKLIN (Department of Biological Sciences, The University of Northern Colorado, Greeley, CO 80639). Growth responses of different aged individuals of *Xanthium strumarium* L. in flooded conditions. J. Torrey Bot. Soc. 141: 72–79. 2014.—In order to assess the effects of age on flooding tolerance, we conducted a mesocosm flooding experiment that examined biomass accumulation of two age cohorts of *Xanthium strumarium* L. We also examined repeated measures of stem height and diameter of each cohort for the duration of the experiment. We hypothesized that change in biomass measures (root and shoot biomass, increase in total biomass, and root shoot ratio) of older individuals would be greater than younger individuals under simulated flooded conditions. We further hypothesized that older individuals would be impacted more than younger individuals regarding stress; i.e., the younger cohort would acclimate and thus flooding effects would be masked. Results indicate that older individuals were more impacted by flooding than younger individuals for all biomass parameters. Height repeated measures indicated that older individuals differentially responded to flooding stress, compared to younger individuals; which was also the case for diameter repeated measures. Our study indicates that individuals exposed to flooding at an early age could be plastically developing acclimation structures leading to younger cohorts subsequently outperforming their older cohorts that did not develop under the stressed conditions.

Key words: Community assembly, diversity, flooding, plasticity, priority effects.

Diversity in floodplain communities is a function of species-specific differences in survival and growth responses to flood disturbance (Crawford 1992, Lenssen et al. 2004, Moore and Franklin 2011), as well as altered interspecific interactions. Many studies suggest disturbance directly weakens competitive effects (Turkington et al. 1993, Wilson and Tilman 1993), while others suggest interactions (competition, facilitation) change along environmental gradients such as salt marsh inundation (Pennings and Calloway 1992), wave exposure (Wilson and Keddy 1986), and nutrient availability (Chesson and Huntley 1997). Plants can cope with competition and stress interactions by switching competitive abilities along the gradient (Suding and Goldberg 2001); for example, weaker competitors (i.e., younger cohorts here) rely upon regular disturbance (increased flood duration) for some competitive release (Huston 1979).

The multi-age structure of populations may alter individualistic responses within the population. Although few studies have examined how competitive abilities and tolerances to disturbance are influenced when conspecifics are different ages (i.e., priority effects), even the slightest difference in germination (Moore and Lacey 2009) and/or arrival time can have a significant impact on competitive outcomes (Mack and Harper 1977, Grace 1985, 1987, Moore and Franklin 2012). For plants, this concept is known as preemption, where the first individuals to arrive inhibit successful colonization by others (Grace 1985). In addition to being ‘larger’, first colonizers can alter nutrient uptake (Chadwell and Engelhardt 2008), root microbial communities (Mayer and Poljakoff-Mayber 1975), and secure rooting space.

Studies have shown that older individuals of ruderal species increase vegetative propagation in response to increased flood duration and delay reproduction events compared to cohorts exposed at an earlier life stage to flooding (Van der Sman et al. 1993). Many species are known to tolerate stressful environmental conditions better after they become more fully established (Grace 1987). Conversely, it has been shown that older individuals exhibit a decrease in

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² Author for correspondence, E-mail: jmoore25@cbu.edu, Fax: 1 (901) 321-4433

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most growth parameters in response to flooding over the short term (Moore and Franklin 2011, 2012). Younger individuals likely respond differently to being exposed at an earlier developmental stage by exhibiting increases in shoot and leaf length (Jackson and Drew 1984, Banga et al. 1995). However, little is known about the interaction between intraspecific competition and priority effects on annual floodplain species’ growth.

To understand how floodplain communities assemble, we must first understand how order of arrival (priority) could potentially affect community structure. For this study, we examined how early arrival of *Xanthium strumarium* L. in controlled conditions could potentially relate to its distribution on Mississippi River islands where flooding stress occurs periodically during the growing season. To explicitly test the role of water stress on the growth between two age cohorts of *Xanthium strumarium*, we experimentally manipulated the order of arrival and quantified age-related growth advantages in lieu of stressors. Hereafter we reference *X. strumarium* by genus only. We measured the effects (or differences) of age (cohort) on biomass accumulation and height and diameter increases under flooding conditions. Specifically, we examined the effects of a two-month ‘head start’ to determine if age confers an increase to stress tolerance. We hypothesized that change in biomass measures (root and shoot biomass, increase in total biomass, and root shoot ratio) of older individuals would be greater than younger individuals under simulated flooded conditions. Previous studies have also shown *Xanthium’s* differential responses to water stresses and competition, with *Xanthium* exhibiting greater biomass when grown with conspecifics compared to heterospecifics. However, these effects of competition were decreased under water stress treatments (Moore and Franklin 2011). We further hypothesized that older individuals would be impacted more than younger individuals regarding stress; i.e., the younger cohort would grow based on their stressor (acclimate) and thus negative flooding effects would be masked.

**Methods. Species Biology.** *Xanthium strumarium* (common cocklebur) is an annual C₃ plant with a facultative wetland (FAC-W) status (USDA NRCS 2012). This plant frequents waste places, roadsides, shorelines of rivers (Löve and Dansereau 1959) and, especially pertinent to this study, occurs in high frequency on Mississippi River islands (Moore et al. 2011). Seed germination can be high (−78%); viability is greatly reduced after 18 months (Weaver and Lechowicz 1982). Seed production ranges from 500 to ~5400 burs plant⁻¹ under optimal conditions (Weaver and Lechowicz 1982). *Xanthium* produces a long taproot with a dense network of finer roots (Reed and Hughes 1970).

**Experimental Design.** This experiment was conducted on the campus of Christian Brothers University, Memphis, Tennessee, USA. The average ambient temperature and precipitation for the duration of the experiment was 23.3 °C and 4.7 cm, respectively (NOAA NOWData www.nws.noaa.gov/climate).

Seeds of *Xanthium* were collected in November 2011 from Dean Island in the lower Mississippi River at river mile 754 (1213 km) (35° 25’ 54.9” N, 90° 0’ 28.0” W). Seeds were collected from a minimum of 10 plants that were located at least 20 m apart. All seeds were cold-stratified at 12 °C for 2 months. Seeds from all sources were mixed before sowing. Seeds of the older cohort were sown on 17 January and seeds of the younger cohort were sown on 17 March. Two weeks after germination of the younger cohort (10 wk post-germination for the older cohort), plants were transplanted into 2.5 L pots (15.24 cm opening, 13 cm base and 17.15 cm tall) containing a 70:30 Quikrete® (Quikrete Concrete Co., Atlanta, GA, US) potting sand and Miracle-Gro® (The Scotts Miracle-Grow Company, Marysville, OH, US) Potting Mix mixture. We examined the effects of water stress (flooding), and cohort status (priority) on *Xanthium* growth. The experiment included a total of 28 pots divided among seven cohort combinations: (1) older + older, (2) younger + younger, (3) younger + older, solitary (4) young or (5) old *Xanthium*, and solitary (6) young or (7) old *Xanthium* that were not included in flooding treatments (i.e., received water ad libitum), with two replicates/mesocosm × two mesocosms, so that *n* = 4 pots/treatment combination. All pots except solitary *Xanthium* pots had two individuals per pot. We did not use controls for all cohort combinations because such combinations were carried out in Moore and Franklin (2011). All pots, excluding controls, were exposed to the same flooding...
regime. Prior to treatments, 10 individuals of each cohort were randomly selected from each cohort (older and younger) and weighed and dried to give beginning total biomass (± 1 SD) for comparison (older = 2.31 g ± 0.197, younger = 1.07 g ± 0.105).

Water Stress. This experiment is part of a series of experiments examining community assembly patterns on Mississippi River islands (see Moore and Franklin 2011, Moore et al. 2011, Moore and Franklin 2012). Mesocosm water stress treatments were used to mimic fluctuations in water levels along a flooding gradient typical of the islands. Durations at intermediate elevations on islands range from 8 to 16 d, and for this experiment flooding lasted 10 d with water levels 5–10 cm above soil surface. Intermittent draining periods lasted for 10 d as well. Although we cannot mimic natural flooding conditions on islands (i.e., flow, sediment and vegetation removal), inundation times were similar.

Biomass Calculations. After 70 d of treatment, plants were extracted, separated into roots and shoots, and dried for 48 h at 80 °C and weighed. Total biomass was calculated as increases (final - initial) in root and shoot weights, and root/shoot ratio was calculated based on final dry biomass. Stem height and diameter were measured prior to and immediately following flooding treatments for each pot (4 floods = 8 measurements pot⁻¹).

Statistical Analysis. We examined the effects of cohort (older or younger or none) in stressed conditions on the dependent variables: root and shoot biomass, increases in total biomass, and root/shoot ratio. General Linear Analysis of Variance (ANOVA) and Multivariate Analysis of Variance (MANOVA) were applied using SAS (SAS 9.1; SAS Institute Inc., Cary, NC, USA 2003). Also, stem height and diameter were analyzed with a Multivariate Analysis of Variance with Repeated Measures (MANOVAR; SAS procedure GLM). Post hoc comparisons were made using a Tukey’s adjustment for multiple comparisons. We also analyzed height and diameter in regards to post-pre flooding, where pre-flooding height and diameter was subtracted from post-flooding height and diameter to gain a better understanding of how different cohorts of Xanthium are affected by flooding. Prior to all analyses, dependent variables were assessed for normality using the PROC UNIVARIATE procedure in SAS to determine if transformations were needed; no variables were transformed. High mortality (reduction from 72 to 28 pots, due to precocious flowering) resulted in low statistical power (height = 0.507, diameter = 0.067), so we adopted a critical alpha level of 0.10. A total of 61 young individuals flowered early (33 during or after the first flood), and 43 old individuals flowered early (36 during or after the second flood). There were no differential responses to cohort combination regarding precocious flowering (F = 2.15, P = 0.150); however, there was significantly greater precocious flowering in flooding treatments (F = 17.65, P = 0.002).

Results. Biomass Measurements. MANOVA results for growth parameters (root and shoot biomass, increase in total biomass, and root shoot ratio) showed a significant cohort effect (Pillai’s Trace F = 4.40, P = 0.02; numerator d.f. = 6); and all individual GLM’s were significant for cohort due to large differences in control pots (root biomass: F = 72.12, P < 0.0001; shoot biomass: F = 190.7, P < 0.0001; root/shoot ratio: F = 5.75, P = 0.001; total biomass: F = 205.9, P < 0.0001; Fig. 1A–D).

Height and Diameter. MANOVAR results indicated a significant increase in height over time (Table 1). Likewise, diameter increased over time, albeit insignificant. There was no significant height × cohort or diameter × cohort interaction (Table 1). Individual GLM’s for height showed differences between cohort, time, and cohort × time interaction. Differences between post-flooding and pre-flooding height were different for older and younger cohorts. Older cohorts actually decreased in height for the second and fourth flood (Fig. 2). Overall, older cohorts were significantly taller than younger cohorts (X = 21.8; 13.93 regardless of time). There were significant differences in post-pre heights for older individuals in floods 1 and 3 versus floods 2 and 4 (Fig. 2). Average cohort height for each measurement was significantly different for the first two floods (measurements 1–4) but not for the third and fourth floods (measurements 5–8; Fig. 3A).

Like height, individual GLM’s for diameter showed a significant cohort, time, and cohort
time interaction. Post-flooding and pre-flooding diameter were different among cohorts, but not for flood or the interactions. Post–pre flooding diameter measurements for the older cohorts were significantly greater (X = 0.622) compared to younger cohorts (X = 0.053; Fig. 4). Average cohort diameter for each measurement was significantly different for the first flood (post–pre) but not for the remaining post–pre combinations (Fig. 3B).

Discussion. To better understand how order of arrival affects single species distribution and competitive ability, we conducted a mesocosm study that examined the effects of priority (2 mo growth ‘head start’) on flooding stress toleration that mimicked hydrologic gradients on Mississippi River islands (Moore et al. 2011). Plants colonizing sites earlier (simulated in a previous study) benefited from a reduction of interspecific competition (Moore and...
Franklin (2012); however, the data do not clearly support this claim for intraspecific competition. In unpredictable environments, such as those at low elevations on Mississippi River islands, frequent occurrence of floods allows frequent re-establishment but may act as a stressor for already established plants (Van der Sman et al. 1993).

Precocious flowering greatly reduced the total number of individuals in this study. Another study focusing on flooding and herbaceous species showed that flooding greatly shortened Chenopodium rubrum L.’s life cycle in older individuals (Van der Sman et al. 1993). Although our results did not show a difference in cohort combination on precocious flowering, the younger cohorts did show greater numbers of flowering individuals (61 younger vs. 43 older individuals). These flowering events occurred during or after the first two floods indicating that stress was a potential factor in precocious flowering. Van der Sman et al. (1993) showed that Rumex palustris Sm. individuals required a minimum leaf number in order to achieve flowering, and in flooded conditions this was delayed, therefore maintaining a vegetative state.

Older individuals in our study maintained their competitive advantage for the first three floods, but the effects of flooding on age were masked during the fourth flood when younger individuals reached the same height and accrued greater stem diameter as older individuals (see Fig. 3A, B). This is consistent with other studies that have examined plant growth in response to flooding. Van der Sman et al. (1993) showed that later cohorts of Rumex spp. allocated more resources into vegetative growth and production of different leaf types under flooded and drained conditions, versus allocating more resources into reproductive parameters.

Interestingly, stress had a greater impact on the older cohort. Previous studies have shown that Xanthium is affected by stress; however, there were stronger competitive interactions when grown with conspecifics compared to

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**Table 1.** General Linear Model (GLM) GLM MANOVAR results for repeated measures differences in height, diameter and the interactions with cohort. Statistically significant $P$-values are indicated in bold, d.f. = Numerator degrees of freedom, and alpha $= 0.10$.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Pillai’s trace</th>
<th>$F$-value</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (cm)</td>
<td>6</td>
<td>4.17</td>
<td>0.006</td>
</tr>
<tr>
<td>Diameter (mm)</td>
<td>6</td>
<td>0.16</td>
<td>0.817</td>
</tr>
<tr>
<td>Cohort $\times$ Height (cm)</td>
<td>6</td>
<td>0.30</td>
<td>0.628</td>
</tr>
<tr>
<td>Cohort $\times$ Diameter (mm)</td>
<td>6</td>
<td>2.19</td>
<td>0.211</td>
</tr>
</tbody>
</table>

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**Fig. 2.** Difference in height (cm) (Post–pre) for old and young cohorts of Xanthium strumarium L. in flooded conditions. Capital letters represent significant differences between floods. Asterisk above line represents significant difference between cohorts (young vs. old) at $\alpha = 0.10$. 

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FIG. 3. Repeated measures averages in pre and post flooding (a) height (cm) and (b) diameter (mm) for *Xanthium strumarium* L during four flooding intervals. Asterisks above flood intervals indicate significant differences between cohorts at that particular flood interval.
heterospecifics, and also greater reduced growth under flooded and drought conditions (Moore and Franklin 2011). Older individuals may be at a disadvantage regarding tolerance of flooding compared to younger individuals. Younger individuals adapt or acclimate to flooded conditions if these conditions occur during early life stages, especially in woody species (Craine and Orians 2006). Annual species in general are at a disadvantage in regards to competition, but this lack of competitive ability may not be important in frequently inundated portions of riverine islands. For plants growing in heterogeneous or disturbed areas, plasticity in ecologically important traits likely contributes to survival and propagation (Mal and Lovett-Doust 2005). Younger Xanthium in our study was exposed to a stressor over a longer period (in terms of whole plant development) of time and therefore was likely subjected to greater cumulative environmental influences, specifically for plant size, and thus showed greater plastic acclimation (Stebbins 1950, Mal and Lovett-Doust 2005). Previous studies have shown significant effects of soil moisture upon vegetative traits, with maximum growth in intermediate soil moisture. Sultan and Bazzaz (1993) studied plasticity in Polygonum persicaria L. in response to light, moisture, and nutrient content of soil where they found marked plasticity in leaf, stem, root, fruit, and in structures related to reproduction following soil moisture changes, but they showed that cohort age was not a factor. In our study, there were no differences across flooding treatments except for older cohorts, illustrating how exposure to a stressor later in development could negatively influence growth. Based on Xanthium being an annual FAC-W plant, there should be an advantage to being older, but that was not the case in our study. When Xanthium competes with heterospecific species, the major advantages it has are seed size and seedling growth (Moore and Franklin 2011).

**Literature Cited**


