



# Phenology of Competitive Interactions and Implications for Management of the Invasive Wetland Plant *Alternanthera philoxeroides*

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**PURPOSE:** Phenological differences between invading plants and members of recipient communities may increase the success of invaders because of priority effects. Thus, the application of management when the invader has a phenological advantage (for example, early in the year) can benefit other species by increasing resource availability. This technical note summarizes results from a combination of field observations and a mesocosm experiment to explore whether phenological differences between the invasive wetland plant, alligatorweed (*Alternanthera philoxeroides* [Mart.] Grseb.), and resident species contribute to alligatorweed success. We documented over two years the early-season growth of alligatorweed and other species at 12 sites in Louisiana, USA. We then conducted a subsequent mesocosm competition experiment between alligatorweed and a common wetland emergent species, spotted lady's thumb (*Persicaria maculosa* [L.] Small), over a full year to detect differences in timing of growth and competitive interactions under two fertilizer levels.

**BACKGROUND:** Many plant invaders are suspected to succeed owing in part to phenological differences with individuals in the recipient community, which may lead to the advantage of resource uptake during periods of the year when other species are not active (that is, the vacant-niche and priority-effects hypotheses) (Xu, Griffin, and Schuster 2007; Gioria, Pyšek, and Osborne 2018; Wolkovich and Cleland 2011; Durham et al. 2017). For example, differences in seed germination or bud burst may benefit an invasive species by reducing the amount of direct competition with other species, thus providing a preemptive advantage to the invader (Gioria, Pyšek, and Osborne 2018; Craine, Dybzinski, and Robinson 2013). In that case, management (for example, biological control) should be applied during the time when invasive species benefit from reduced competition and are actively growing and spreading, shifting dominance away from the invader and back to the native community (Alexander and Levine 2019; Fridley and Craddock 2015; Godoy and Levine 2014). Early growth relative to members of the invaded community may have evolved to avoid negative effects from competitive interactions with other species (Wolkovich and Cleland 2014). In fact, evolution of the early-growth life history trait in invaders (that is, competition avoidance) may be an adaptive response to strong competition in the native range (Gioria and Osborne 2014).

Taking into account demographic processes and the phenology of invasive species has provided valuable insights into the management of a number of terrestrial and aquatic systems (Marushia, Cadotte, and Holt 2010; Byers et al. 2002; Emery and Gross 2005; Ramula et al. 2008). In particular, aquatic and wetland invasive plant managers now understand that patterns of plant growth, nutrient allocation, and reproduction are all important to consider when prescribing management of plant invaders while limiting negative impacts to nontarget species (Mudge, Perret,



and Winslow 2016; Wersal and Madsen 2018; Nichols 1991; Madsen and Owens 1998). However, putting into practice the exploitation of phenological differences between invasive and native species is still not widespread (Wersal and Madsen 2018). One limitation may be that invaders are the focus of phenological studies, whereas members of invaded communities often are not. Another limitation is that phenological studies of aquatic plant invaders are often restricted geographically, constrained to a small area within the invaded range, limiting the geographic scope of inferences resulting from many phenological studies. Studies that combine field observations of resident and invader phenologies across the geographic range of the invader with experimental tests of differences in phenology are even rarer.

Using the wetland plant invader alligatorweed, we used a combination of field observations and a mesocosm experiment to test whether a difference in phenology between an invader and recipient community is a primary determinant for successful invasion. We studied alligatorweed and resident wetland plant species in established infestations in Louisiana for two years to document differences in timing of growth. To complement field observations, we conducted an outdoor mesocosm experiment in southern Louisiana to examine phenology and associated competition between alligatorweed and the common wetland plant, *Persicaria maculosa* (spotted lady's thumb) under two levels of fertilizer (low, high). We predicted that (1) alligatorweed would be a dominant species in natural and mesocosm communities because of early-season biomass production and (2) that alligatorweed would be the superior competitor in the mesocosm experiment, particularly under low (that is, limiting) nutrient conditions.

## MATERIALS AND METHODS

**Study System.** Alligatorweed was introduced into the United States from South America over 100 years ago and is now present in every southeastern state and California (Spencer and Coulson 1976). Alligatorweed has been a successful invader, in part because it can rapidly establish new populations through clonal reproduction, is tolerant of environmental fluctuations, and has a geographic range in the United States that extends beyond the range of its introduced biological control agents (Buckingham, Doucias, and Theriot 1983; Buckingham and Boucias 1982; Shen et al. 2005; Harms and Cronin 2020). In tropical areas, alligatorweed is perennial, but in temperate areas, it is an annual and recovers in spring from underground root stock produced during the previous year instead of growing from seeds (Shen et al. 2005). Little information on the timing of alligatorweed growth in the United States currently exists, but Vogt, Quimby, and Kay (1992) suggested that alligatorweed grows rapidly in early to late spring—a trait that may contribute to its invasiveness—although peak growth in invaded Chinese wetlands occurred during summer months (Shen et al. 2005). If alligatorweed growth commences earlier than potential competitors in the introduced range, high efficacy of introduced biological control agents (for example, *Agasicles hygrophila* Selman and Vogt) may be related to their early-season defoliation in areas where they overwinter or disperse in spring (Harms and Shearer 2017; Vogt, Quimby, and Kay 1992; Harms and Cronin 2020). Management, by biological control or herbicides, may be most effective in concurrently controlling alligatorweed and supporting native species recruitment if applied during the period of early-season growth (Allen, Hepp, and Miller 2007).

**Field Survey.** To document the phenology of alligatorweed and potential competitors in invaded communities, we first conducted field surveys across the range of alligatorweed in Louisiana (Figure 1). We chose survey site locations to span the range of climates experienced in the state

and visited sites approximately once every three weeks for two growing seasons (spring–fall, 2016 and 2017) to document potential year-to-year variation in phenology. During site visits, we randomly placed four 1/10 m<sup>2</sup> square polyvinyl chloride (PVC) frames within alligatorweed infestations then counted alligatorweed emergent stems and the number of other emergent or floating plants.<sup>1</sup> Because phenology of plants varies with climate (Bertin 2008), we grouped sites into southern, central, and northern geographical regions within the state for comparisons (Figure 2). This area largely encompasses the range of climates experienced by *A. hygrophila* in the United States. We used mean stems per square meter for each site and date to calculate regional means and present the data here as time series for each region for each year.

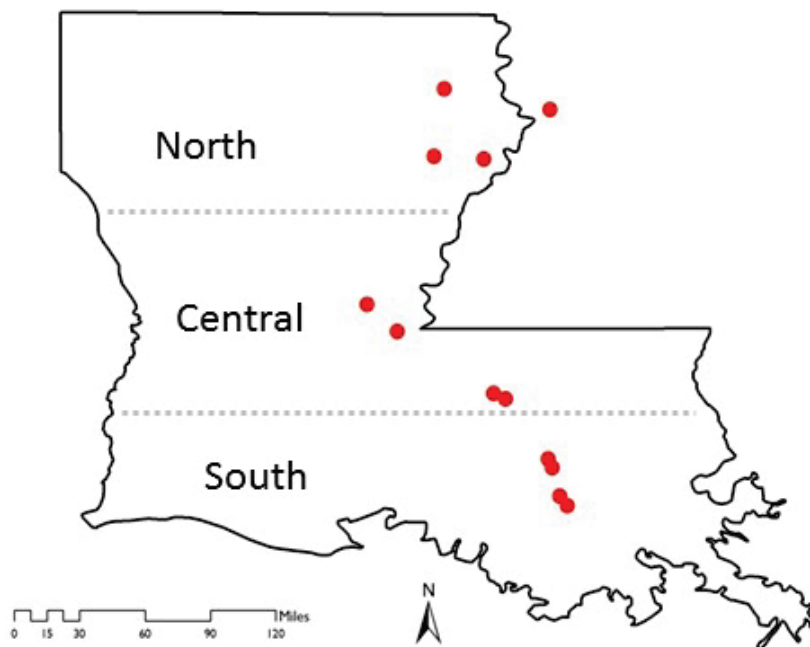


Figure 1. Study sites (red circles) in Louisiana grouped by region in the state.

**Mesocosm Experiment.** We designed the competition experiment to document the timing of growth and resource-based competition between alligatorweed and the naturalized spotted lady's thumb (*Persicaria maculosa* [L.] Small), an annual wetland plant common in Louisiana that often co-occurs with alligatorweed in wetland habitats. We collected experimental plants of both species from a public pond in Simmesport, Louisiana, (N 30.97°, W 91.81°) and cultured them in a greenhouse for more than a year prior to use to minimize maternal effects (Roach and Wulff 1987). Culture consisted of floating plants in 20 L plastic containers filled with a modified Hoagland's media (Hoagland and Arnon 1950). One month before the experiment, we propagated the plants several times to produce enough experimental material. Approximately one

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<sup>1</sup>. For a full list of the spelled-out forms of the units of measure used in this document, please refer to *US Government Publishing Office Style Manual*, 31st ed. (Washington, DC: US Government Publishing Office, 2016), 248–52, <https://www.govinfo.gov/content/pkg/GPO-STYLEMANUAL-2016/pdf/GPO-STYLEMANUAL-2016.pdf>.

week before the experiment, we floated the plant propagules in water to allow adventitious root formation, then subsequently planted (see below).

Experimental design was a  $2 \times 2$  factorial, consisting of competition (two levels: each species grown alone or with the other) and fertilizer (two levels: low or high) treatments. Experimental setup took place in late fall 2016 in an outdoor plot at the Louisiana State University Innovation Park (N 30.36°, W 91.14°). The fall planting allowed natural timing of growth the following spring while establishing plants in mesocosms before winter. We planted propagules (a single 15 cm apical fragment with roots) either alone or together in 3.78 L nursery pots filled with 2 L builder's sand combined with 5 g (low) or 20 g (high) Osmocote Plus (15-9-12) slow-release fertilizer. At planting, we recorded initial fresh weights of both species (mean alligatorweed initial mass =  $1.52 \pm 0.45$  g; mean spotted lady's thumb initial mass =  $2.76 \pm 0.83$  g). We kept plant propagules intentionally small to reduce, as much as possible, propagule-size effects on the outcome of the experiment. The planted pots we placed individually in 20 L plastic mesocosms, which we placed on a grid and arranged in a completely randomized design (using a random number generator) on the outdoor plot. We added water to approximately 20 cm above the sediment surface in each mesocosm and maintained it at that level during the experiment. The following spring (March 2017), we conducted stem counts in each mesocosm, which consisted of stems emerging above the water surface and then conducted stem counts again in summer (July 2017) and fall (October 2017), prior to harvest. Harvest consisted of removing plants, separating species into above- and belowground tissues, rinsing them, and placing them in labeled paper bags for drying. We, then, dried the plants at 60°C to constant weight and weighed them to the nearest 0.01 g.

We assessed the factors influencing plant abundance during the experiment using a general linear model repeated measures Analysis of Variance (ANOVA), with date (D) as the repeated measure and community composition (C) and fertilizer (F) as main effects. We also included in the model all possible interactions among these terms along with initial weights of both species as covariates. We conducted separate analyses for biomass at harvest. Here, we used a general linear model that included the same predictor variables as above except for date. For the first analysis (over time) we used log-transformed stem density as the response variable. In the second analyses (at harvest), we used log-transformed total biomass and shoot:root ratio as response variables. The statistical analyses were performed using Statistica version 12 (Statsoft 2013) at  $\alpha = 0.05$ .

Additionally, to assess the strength and symmetry of competition at the different fertilizer levels, we calculated relative interaction intensities (RII) for each species (Armas, Ordiales, and Pugnaire 2004) using harvest biomass measurements. RII has a value between  $-1$  and  $+1$ , with negative values indicating competition and positive values indicating facilitation. RII is calculated as

$$RII = \frac{B_w - B_o}{B_w + B_o} \quad (1)$$

where  $B_w$  is the mass of a plant grown in the presence of others and  $B_o$  is the mean mass of plants of the same species grown alone (Cavieres et al. 2004). *RII* was calculated for both species, and *RII* at harvest was compared between species at low and high fertilizer levels using two-way ANOVA.

## RESULTS

**Field Survey.** Abundances of alligatorweed and other species were variable within and between years and regions within Louisiana (Figure 2). Overall abundance of alligatorweed was highest in northern areas. This may have been due to the lack of consistent biological controls in these areas (Harms and Shearer 2017; Harms and Cronin 2020). In all three areas, alligatorweed growth began early (February) but peaked early only in southern areas. In central and northern Louisiana, the date of peak alligatorweed abundance ranged from early (April in central Louisiana in 2017) to mid-summer (Northern Louisiana in 2016) to no distinct peak (central Louisiana in 2016). Similarly, peak abundance of other species in the study sites was recorded early in southern locations (Figure 3A and B) both years. In central Louisiana, abundance of other species was gradual but never reached distinct peaks either year. In northern sites, peak abundance occurred in midsummer (2016) or late spring (2017).

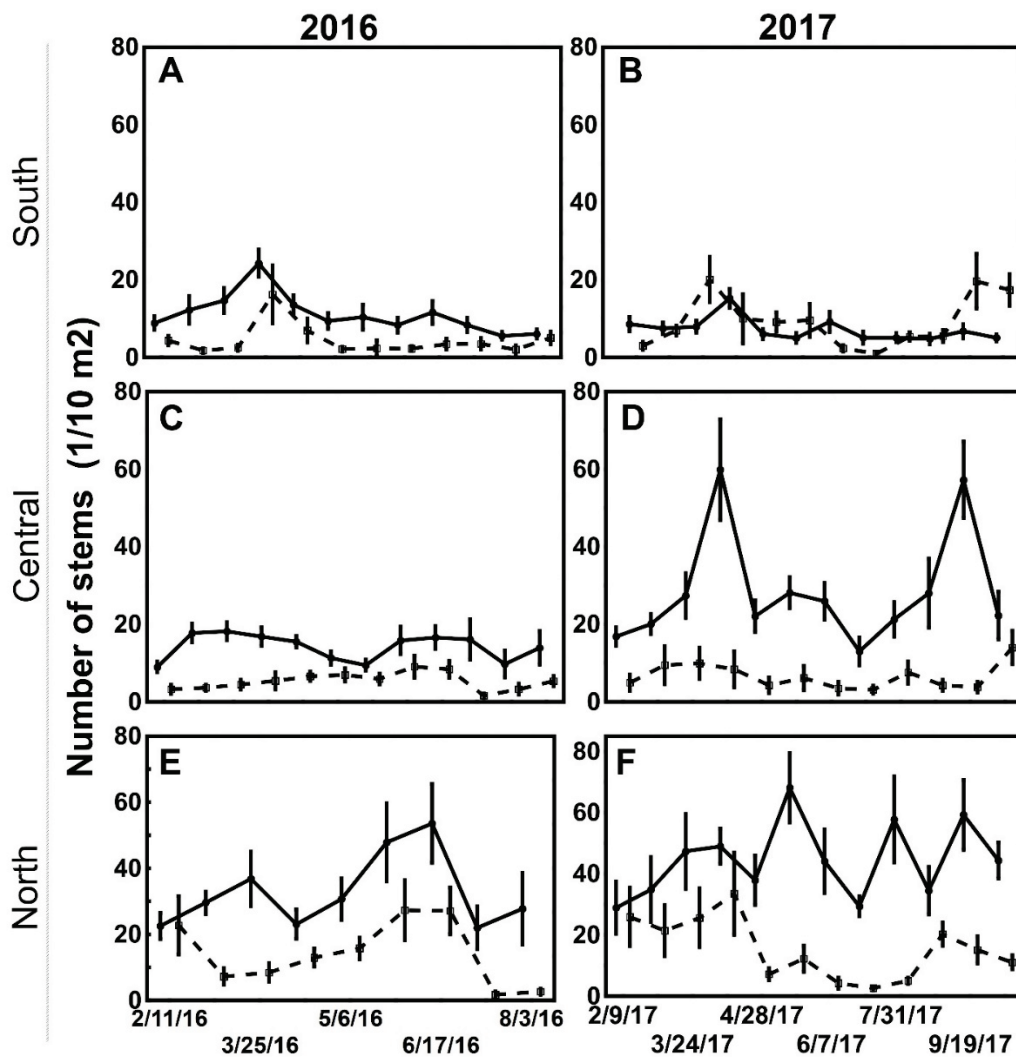


Figure 2. Abundance (mean  $\pm$  SE) of alligatorweed (solid line) and other species (dashed line) averaged over study sites in each region of Louisiana in 2016 (A, C, E) and 2017 (B, D, F).

**Mesocosm Experiment.** For both species, fertilizer level, competition, date, and the interactions between fertilizer and season and competition and date had significant effects on abundance in the mesocosm experiment (Table 1). There were phenological differences between the species in peak abundance (Figure 3); alligatorweed maximum abundance occurred in spring in the high-fertilizer alligatorweed monoculture treatment ( $43.5 \pm 4.2$  stems mesocosm<sup>-1</sup>;  $589 \pm 33.9$  stems m<sup>-1</sup>; Table 1; Figure 3a), whereas spotted lady's thumb abundance peaked during summer in the high-fertilizer monoculture treatment ( $50.7 \pm 7.8$  stems m<sup>-1</sup>; Table 1; Figure 4b).

<b>Table 1. Repeated-measures ANOVA table for alligatorweed and spotted lady's thumb stem abundance during competition study. F = fertilizer, C = competition, D = date.</b>						
Treatment	<i>Alternanthera philoxeroides</i>			<i>Persicaria maculosa</i>		
	Log (abundance)			Log (abundance)		
	F	df	p	F	df	p
F	84.42	1	<0.001	39.77	1	<0.001
C	115.65	1	<0.001	10.34	1	0.002
D	34.82	2	<0.001	55.57	2	<0.001
F×C	3.02	1	0.09	0.11	1	0.75
F×D	10.67	2	<0.001	4.77	2	0.01
C×D	8.19	2	<0.001	5.14	2	0.01
F×C×D	0.88	2	0.42	0.2	2	0.82

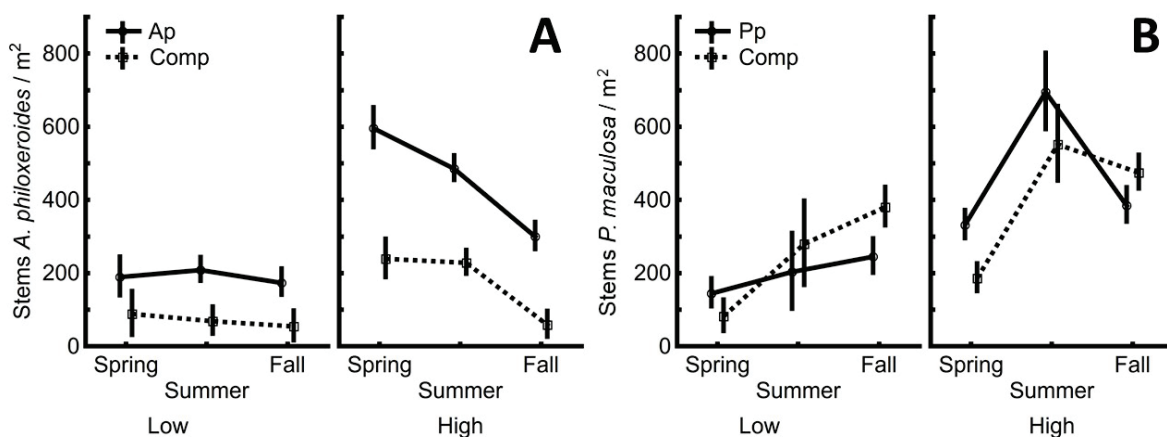


Figure 3. Seasonal stem abundance (mean ± SE) for *A. philoxeroides* (Ap) and *P. maculosa* (Pp) grown in monoculture or under competition (Comp) at low and high fertilizer levels. Means were adjusted to account for initial differences in the weights of each species.

Biomasses of spotted lady's thumb and alligatorweed were similar when grown in monoculture at low-nutrient conditions, but spotted lady's thumb had 83% more biomass than alligatorweed in monoculture in high-nutrient conditions. In addition, spotted lady's thumb had 102% and 263% more biomass under competition in both low- and high-nutrient conditions, respectively (Figure 5). Fertilizer significantly increased biomass in both species (Table 2; Figure 5). Interestingly,

under the competition treatment, we detected differences in total biomass for alligatorweed only and differences in shoot:root ratio in spotted lady's thumb only, highlighting the differential effects of competition on biomass allocation between species (Table 2). For spotted lady's thumb, allocation to aboveground versus belowground biomass shifted with fertilizer (low fertilizer shoot:root ratio:  $1.09 \pm 0.14$ ; high fertilizer shoot:root ratio:  $1.60 \pm 0.14$ ). In contrast, biomass allocation in alligatorweed consistently favored roots, regardless of fertilizer or competition treatment.

<b>Table 2. ANOVA table results for alligatorweed and spotted lady's thumb biomass metrics. F = fertilizer, C = community, D = date, DW = dry weight.</b>						
<i>Alternanthera philoxeroides</i>						
Treatment	Log(total DW)			Shoot:root		
	F	df	p	F	df	P
F	8.75	1	0.01	0.19	1	0.66
C	10.69	1	0.002	0.03	1	0.87
F×C	1.93	1	0.17	0.3	1	0.59
<i>Persicaria maculosa</i>						
	Log(total DW)			Shoot:root		
	F	df	p	F	df	p
F	109.47	1	<0.001	7.02	1	0.01
C	1.73	1	0.2	6.33	1	0.02
F×C	0.36	1	0.55	0.16	1	0.44

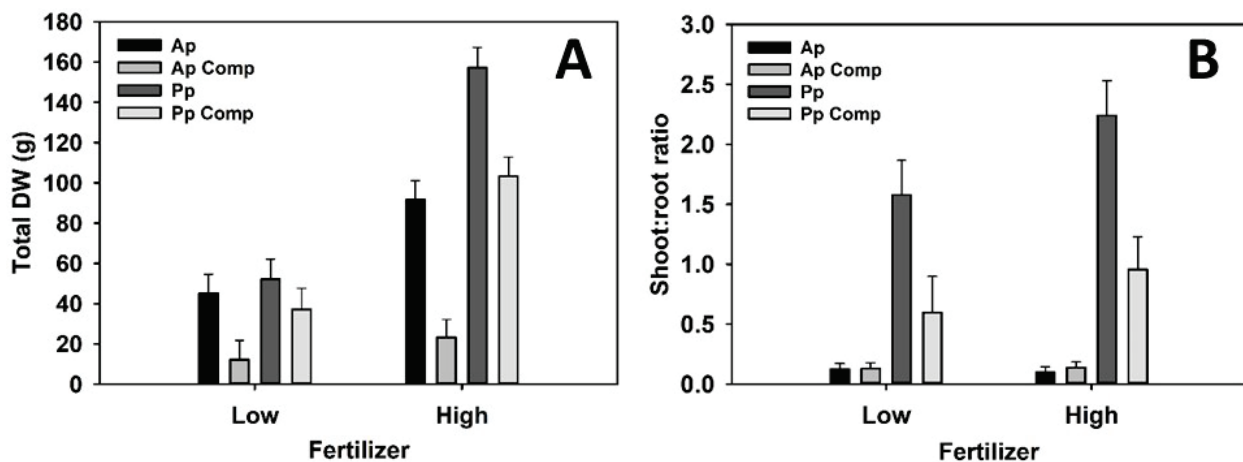


Figure 4. Mean  $\pm$  SE total dry weight (DW) biomass (A), and shoot:root biomass ratio (B) for alligatorweed and spotted lady's thumb alone (Ap, Pp) or under competition (Ap Comp, Pp Comp) and low or high nutrients. Least squared means were calculated to account for initial weights.



In contrast to our prediction, and despite earlier growth, alligatorweed was not the dominant species when grown in competition with spotted lady's thumb. RII values were asymmetric between competitors, with alligatorweed affected more by competition ( $RII = -0.44 \pm 0.04$ ) than spotted lady's thumb ( $RII = -0.16 \pm 0.04$ ) and the largest effect from competition for alligatorweed grown in the high-fertilizer treatment ( $RII = -0.51 \pm 0.06$ ) (Figure 5). RII was significantly influenced by species identity but not fertilizer level or the interaction between species and fertilizer (two-way ANOVA; species:  $F = 19.03$ ,  $df = 1$ ,  $p < 0.001$ ; fertilizer:  $F = 3.06$ ,  $df = 1$ ,  $p = 0.09$ ; species  $\times$  fertilizer:  $F = 0.57$ ,  $df = 1$ ,  $p = 0.45$ ).

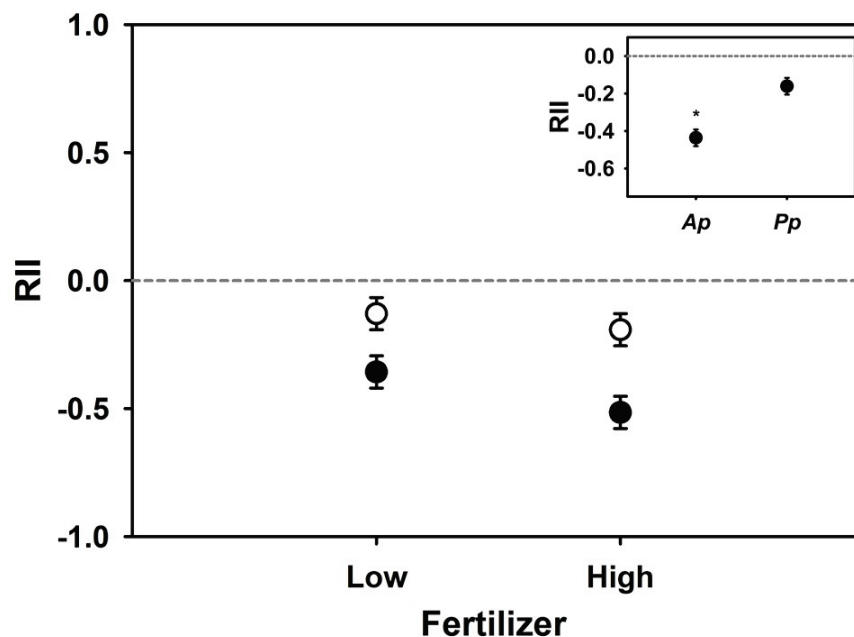


Figure 5. Mean  $\pm$  SE relative interaction intensity (RII) calculated for alligatorweed (black points) and spotted lady's thumb (white points) grown together under low or high fertilizer levels. Shown in the inset is the species mean RII. The asterisk in the inset signifies different means (two-way ANOVA;  $F = 19.03$ ,  $df = 1$ ,  $p < 0.001$ ).

**DISCUSSION:** At field sites, alligatorweed was consistently the dominant species. However, because we chose sites for alligatorweed presence, our site selection may have biased the results towards locations where alligatorweed was already dominant. Regardless, we demonstrated spatial heterogeneity of phenology in alligatorweed in Louisiana, with southern sites growing earlier in the season than in northern locations, but we did not detect a consistent pattern in the phenology of invaded communities. In a mesocosm experiment, phenological differences in growth (maximum abundance in spring versus summer) between the wetland invader, alligatorweed, and the naturalized spotted lady's thumb did not lead to the expected competitive outcome between species. Despite seasonal differences in growth (for example, maximum abundance of alligatorweed in spring, 15 weeks earlier than spotted lady's thumb in summer) alligatorweed was 45% more affected by competition and was a relatively poor competitor, at least under the conditions (competitor species, water level, climate, lack of herbivory, single year) in our experiment. Alligatorweed's competitive strength (measured either as negative effects of



alligatorweed on other species or negative effect of other species on alligatorweed) has been investigated for its role in invasion success in some areas (Allen, Hepp, and Miller 2007; Adams 2011, Wundrow et al. 2012). For instance, Adams (2011) tested whether competition from native species in combination with herbicide application might be valuable to manage alligatorweed infestations and determined that only herbicides were effective to reduce alligatorweed abundance (that is, alligatorweed was unaffected by competition from native species). However, that study examined introduction of competitors to well-established alligatorweed infestations, and no data existed on resource availability at or after competitor introduction. In contrast, Allen, Hepp, and Miller (2007) provided a convincing account of the importance of competition and timing of management in alligatorweed success. In field locations, they applied varying concentrations of herbicides at two times during the growing season (April, July) and found significant short-term (measured in October of the same year) reduction in alligatorweed abundance coupled with enhanced native species abundance in the earlier, but not later, treatments. However, when evaluating the communities a year after treatment, results varied much more, with native species abundance greater in plots treated during the later time period. Despite some support for enhanced competitive ability of alligatorweed, others have found reduced competitive abilities, for instance against other invaders (Wundrow et al. 2012). For example, the presence of water hyacinth (*Pontederia crassipes* [Mart.] Solms) reduced alligatorweed abundance at a study site in Texas, despite the apparent positive effect of alligatorweed on water hyacinth (Wundrow et al. 2012). In the current study, and despite the high impact of competition on alligatorweed, proportional allocation of biomass to roots was high in both alligatorweed monoculture and in competition. If our experiment had continued for a second year, the enormous allocation of resources to root stock may have disproportionately benefited alligatorweed over the annual competitor. This pattern of biomass allocation also leads to the prediction that alligatorweed establishment in a new location may not appear substantial according to aboveground structures but may quickly increase during subsequent years because of substantial underground energy storage.

In the current study, we demonstrated that, when introduced together and allowed to grow over a single year, alligatorweed was the inferior competitor, despite numerical dominance in field locations. A factor that we did not focus on but, which may prove informative for future studies, is in the importance of environmental heterogeneity in alligatorweed success. Alligatorweed has high plasticity in response to resource availability (soil moisture, light, nutrients) (Bassett, Paynter, and Beggs 2011; Geng et al. 2016), and competitive effects of alligatorweed on native species have been found to depend largely on environmental heterogeneity (Liu et al. 2016). The variability we observed in field sites with regards to alligatorweed dominance and apparent discrepancy with the mesocosm experiment may be largely due to our maintenance of relatively homogeneous conditions in the mesocosm experiment versus heterogeneous conditions in the field. For example, although we maintained water levels within 10–20 cm throughout the mesocosm experiment, water depth fluctuated greatly among and within field sites. For example, at Blind River, Louisiana, water depth fluctuated 70 cm and 115 cm during the 2016 and 2017 growing seasons, respectively. Perhaps a more realistic test of competitive ability and alligatorweed invasion would include a disturbance treatment with control, such as variable or stable water levels, or to conduct a similar competition study in situ, with plant removal or addition treatments.

Competitive interactions between species are influenced by various biotic and abiotic aspects of their environment, including predation or herbivory (Louda, Keeler, and Holt 1990). The plants in our experiment were mostly free of herbivory, but we observed transitory and limited feeding by

generalists (for example, fall armyworm, *Spodoptera frugiperda* [J.E. Smith]) and a few specialists (alligatorweed flea beetle, *Agasicles hygrophila*). How a reduction of herbivory affects competition between alligatorweed and spotted lady's thumb relative to competition in the presence of herbivory is unknown but provides future research directions. Although there are no good records of herbivores associated with spotted lady's thumb in the United States, there are a number of generalist and specialist herbivores of other *Persicaria* spp. (Harms and Grodowitz 2009). If herbivore pressure under field conditions is high, then removing them during our experiment may have led to increased spotted lady's thumb performance. Future experiments should take place in a natural setting where herbivory (especially biological control) on all species can occur and be measured as a covariate.

The evolution of phenology to avoid negative interactions with other organisms may be a driver of success for some invasive species. In the case of alligatorweed, early growth may only be advantageous in some areas and is likely not a major factor in the widespread success of alligatorweed. In contrast, the ability to colonize disturbed habitats and biomass allocation towards vegetative reproduction may be more important to explain dominance in some areas, particularly where alligatorweed has been established for multiple years. Thus, management of new populations will likely provide the greatest potential for control, especially where a pool of potential competitor species exists. Established populations, although likely more difficult to control, may benefit from early season management, during the time when alligatorweed is producing new stems and competition with other species is uncommon.

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