

# Competition, salinity, and clonal growth in native and introduced irises<sup>1</sup>

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**PREMISE OF THE STUDY:** *Iris pseudacorus* spread rapidly into North America after introduction from Europe in the 1800s and now co-occurs with native *I. hexagona* in freshwater Louisiana wetlands. Native irises support and interact with multiple trophic levels, whereas *I. pseudacorus* is classified an invasive pest because it grows aggressively, reduces biodiversity, and displaces native vegetation. Salinity levels are increasing in coastal wetlands worldwide. We examined how salt-stress affects competitive interactions between these conspecifics.

**METHODS:** We established a three-way full-factorial common-garden experiment that included species (*I. pseudacorus*, *I. hexagona*), competition (no competition, intraspecific competition, and interspecific competition), and salinity (0, 4, 8 parts per thousand NaCl), with six replicates per treatment.

**KEY RESULTS:** After 18 mo, *Iris pseudacorus* produced much more biomass than the native species did ( $F_{1,92} = 71.5, P < 0.0001$ ). Interspecific competition did not affect the introduced iris, but biomass of the native was strongly reduced (competition  $\times$  species interaction:  $F_{2,95} = 76.7, P = 0.002$ ). Salinity significantly reduced biomass of both species ( $F_{2,92} = 21.8, P < 0.0001$ ), with no species  $\times$  salinity interaction ( $F_{2,84} = 1.85, P = 0.16$ ).

**CONCLUSIONS:** Our results demonstrate that salt stress strongly reduced clonal reproduction in native and introduced irises; however, the introduced iris had a competitive advantage over the native, regardless of environmental salinity levels. Based on patterns in clonal reproduction, the introduced iris could potentially threaten native iris populations. We are currently investigating seed production and mortality during competition and stress because both clonal and sexual reproduction must be considered when predicting long-term population dynamics.

**KEY WORDS** clonal reproduction; coastal wetlands; environmental disturbance; interspecific competition; invasive plants; Iridaceae; *Iris hexagona*; *Iris pseudacorus*; salinity stress

Many studies have documented the negative impacts of invasive species (Mack et al., 2000; Simberloff, 2000; Leger, 2008), which can devastate the ecological health and economic value of ecosystems (Williamson and Fitter, 1996; Lonsdale, 1999). Wetlands in particular are vulnerable to invasion by introduced plants and animals (Stephens and Sutherland, 1999; With, 2002; Zedler and Kercher, 2004). Factors that influence the spread of exotic species include light (Keane and Crawley, 2002), nutrients (Lake and Leishman, 2004), natural enemies (Davis et al., 2000), and management practices

(Chmura and Sierka, 2007). Some exotic species have higher population growth rates than native populations (Loehle, 1987) and a greater potential to rapidly colonize available habitat (Taylor et al., 2004).

In Louisiana, a native (*Iris hexagona* Walter, Iridaceae; blue flag iris) and introduced (*I. pseudacorus* L., Iridaceae; yellow flag iris) iris frequently coexist in inland freshwater habitats. The native iris (Fig. 1) is an important member of a diverse wetland community, supporting and interacting with multiple trophic levels (Carlton et al., 2000; Geddes and Mopper, 2006; Tobler et al., 2006; Wang and Mopper, 2008). *Iris pseudacorus* is indigenous to Europe and Asia and has a cosmopolitan distribution (Crawford, 2000; Mehroff et al., 2003). Because of its showy flowers (Fig. 1), it was introduced as an ornamental from Europe in the early 1800s and occurs in 46 states and Canada (Cody, 1961; Sutherland, 1990). The introduced iris is considered an invasive pest in many states because it reduces ecological biodiversity, clogs waterways, increases sedimentation, and disrupts natural landscapes (Preece, 1964; Raven and Thomas, 1970; Crawford, 2000; USDA NRCS, 2002).

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**FIGURE 1** Native *Iris hexagona* (left) and introduced *Iris pseudacorus* (right), which are similar in aboveground size and morphology. Photo by Karl Hasenstein.

*Iris hexagona*, series *Hexagonae*, is in a monophyletic complex of five species and associated hybrids, known as Louisiana irises (Meerow et al., 2011). Our previous work demonstrated profound effects of salinity on *I. hexagona* physiology, ecology, and reproduction (Wang et al., 2001, 2008; Van Zandt and Mopper, 2002, 2004; Van Zandt et al., 2003; Mopper et al., 2004; Geddes and Mopper, 2006; Schile and Mopper, 2006; Tobler et al., 2006; Wang and Mopper, 2008; Pathikonda et al., 2008, 2010). The co-occurrence of *I. pseudacorus* with the endemic *I. hexagona* in many Louisiana freshwater wetlands allows a direct comparison of conspecifics with similar life cycles and habitat preferences (Garcia-Serrana et al., 2007). To our knowledge, no hybridization events between the introduced and native species have been reported, nor have we observed hybridization between them.

*Iris pseudacorus* is reported to grow best in freshwater or low-salinity marsh and may have limited salt tolerance (Sutherland and Walton, 1990). In contrast, *I. hexagona* populations inhabit freshwater, intermediate, and brackish Louisiana wetlands (Van Zandt and Mopper, 2002, 2004; Van Zandt et al., 2003). Because of its reported negative effects on other ecosystems, the potential exists for *I. pseudacorus* to impact native Louisiana iris populations and wetland communities (Crawford, 2000; USDA NRCS, 2002; Mehroff et al., 2003). However, it has not yet invaded intermediate-salinity (2–8 parts per thousand (ppt)) coastal Louisiana wetlands, which contain many native iris populations (Wiens, 2009).

We conducted a full-factorial common-garden experiment to examine the performance of *I. pseudacorus* and *I. hexagona* grown together and separately in freshwater and salinity treatments. On the basis of published observations and population growth models

(Sutherland and Walton, 1990; Pathikonda et al., 2008), we predicted that the introduced iris would outcompete the native in freshwater and that the native would outcompete the introduced in elevated salinity conditions. This study provides insight into how an abiotic disturbance such as salinity, which is increasing throughout the globe, could influence interactions between native and introduced plants, and their long-term population dynamics.

## MATERIALS AND METHODS

**Natural history**—*Iris pseudacorus* grows in a variety of habitats, from rocky shorelines to organic soils (Thomas, 1980). Plants develop thick clonal ramets that produce flowering stalks in the first or second year of growth. Multiple ramets may remain attached for long periods but eventually can separate into independent units that retain the same genetic composition as the original ramet (Sutherland and Walton, 1990). The 1-m-tall flower stalks each produce multiple large, yellow inflorescences yielding 6–12 seed capsules, each containing 80–120 seeds. In Louisiana, flowering occurs during March and April, and phenology is influenced by abiotic factors such as temperature or flooding (Dymes, 1920; Sutherland, 1990). Seeds, which are sexual propagules, and rhizomes, which are clonal propagules, are both water-dispersed (Coops and Vandervelde, 1995).

*Iris hexagona* is endemic to marshes and riparian zones in North America (Bennett and Grace, 1990; Meerow et al., 2011). In Louisiana, large, expansive populations inhabit freshwater and intermediate-salinity coastal marsh, and smaller colonies occur in brackish wetlands (Van Zandt and Mopper, 2002). Similar to *I. pseudacorus*, *Iris hexagona* blooms in March and April, producing flowers that are pollinated by bumblebees. The 1-m-tall flower stalks each produce 4–6 blue flowers that yield seed capsules with 40–60 seeds (Van Zandt et al., 2003). Although similar in aboveground size and appearance, several traits distinguish the native from the introduced species, respectively: blue vs. yellow flowers, ovoid vs. narrow seed capsules, flat leaves vs. leaves with pronounced midvein, white vs. orange rhizome tissue.

**Experimental design**—We conducted a common garden study at the University of Louisiana Ecology Center in Lafayette, Louisiana from March 2006 to July 2008 (see Van Zandt et al. [2003] for additional methods). We established a three-way full-factorial design with replication that included three main effects: species (*Iris pseudacorus* and *I. hexagona*), competition (no competition, intraspecific competition, and interspecific competition), and salinity (0, 4, and 8 PPT). We started with six replicate containers for each treatment, for a total of 90 containers. We placed the 120 diameter × 30 cm tall round, plastic containers 3 m apart in a rectangular grid in a mowed old-field habitat. Each container was partially submerged in the ground, filled to a height of 20 cm with topsoil, and encircled with sandbags for protection from mowing equipment.

We inserted a 15 × 7.5 cm polyvinyl chloride pipe drilled with holes and covered with nylon mesh into the center of each container to allow regular monitoring of interstitial soil salinity. Containers were randomly assigned to treatments.

In March 2006, we collected *I. pseudacorus* and *I. hexagona* plants from multiple field populations in southwestern Louisiana. After removing leaves and roots, we cut an 8–10 cm length of rhizome from each plant. We weighed then planted the rhizome segments in the containers approximately 2 cm below the soil surface. The number of rhizomes planted per container was determined by the competition treatment (no competition = a single *I. pseudacorus* or *I. hexagona* rhizome, intraspecific competition = four rhizomes of the same species, and interspecific competition = two rhizomes of each species). Final results for each replicate treatments were averaged within containers, then standardized to estimate the growth of a single rhizome. There was mortality of some planted rhizomes during initial stages of the experiment; thus, the number of replicates is unequal. All treatments were replicated by a minimum of four containers.

We watered plants regularly with an automated sprinkler system and mowed the area around each container fortnightly. Soil was kept moist and salinity levels adjusted as necessary to maintain treatments (see Van Zandt et al., 2003 for detailed methods). Planted rhizomes produced new growth in fall 2006. All containers received full sun and were not shaded by other plants.

**Competition**—Containers were assigned to one of three different treatments: no competition (a single *I. pseudacorus* or *I. hexagona* rhizome), intraspecific competition (four rhizomes of the same species), and interspecific competition (two rhizomes of each species (interspecific competition)). We planted the no-competition rhizomes near the center of the container. Rhizomes in the intra- and interspecific competition treatments were placed singly in each quadrant of the container. Species in the interspecific treatment were alternated.

**Salinity**—In January 2007 we established 0, 4, and 8 ppt salinity levels using Instant Ocean Artificial Sea Salt (Spectrum Brands, Atlanta, Georgia, USA). We monitored mesocosms weekly using a portable YSI model 30 device (Yellow Springs, Ohio, USA) and adjusted salinity as necessary to sustain the treatment levels.

**Statistical analyses**—We harvested plants in June–July 2008, carefully rinsed them thoroughly to remove soil, separated leaves, roots, and ramets, and air-dried all material for several weeks before weighing. We measured foliage, root, and ramet mass (g) and counted the number of ramets produced by the original rhizome segment. Plants were averaged within containers, resulting in one data point per factor/treatment per replicate to avoid pseudoreplication (Hurlbert, 1984). We standardized all data to reflect the performance of a single rhizome. For example, in an intraspecific treatment container with four rhizomes, we divided the data collected by 4; in the interspecific treatment containers, we divided data from each species by 2; and the no-competition treatment containers were not adjusted since they contained a single rhizome. We applied log-transformation to all variables, which successfully normalized data to conform to parametric assumptions. The data illustrated here in figures are presented in their nontransformed state as means ± SEs in grams.

We tested the separate and interactive effects of species, salinity level, and competition on plant growth and included initial

rhizome mass as a covariate (SAS, 2015). Because all variables were highly positively correlated (Table 1), we summed the biomasses of leaves, ramets, and roots to create a new variable, total biomass (g), which we used to quantify plant performance. We first ran a fully saturated ANCOVA that included the original mass of the planted rhizomes as a covariate, and all possible interactions among the three main effects. We then removed nonsignificant variables from the model and reran the analysis. We used type III sums of squares (SS) in all ANOVAs and employed Tukey-adjusted pairwise comparisons to test differences between treatments within factors.

**RESULTS**

Leaf mass comprised only 0.7% of total biomass; thus, the vast majority of plant biomass occurred belowground (Fig. 2). The fully saturated three-factor model with all possible interactions was highly significant ( $F_{18, 84} = 8.6, P < 0.0001$ ). The initial mass of planted rhizomes was greater for introduced than native irises ( $56 \text{ g} \pm 3.4 \text{ SE}$  and  $31 \text{ g} \pm 1.0 \text{ SE}$ , respectively,  $t = 7.0, n = 103$ ), but initial rhizome mass had no significant effect on final plant biomass according to the ANCOVA analysis ( $F_{1,84} = 2.2, P = 0.15$ ).

**Interactions**—There was a significant species × competition interaction ( $F_{2, 95} = 6.7, P = 0.002$ , Fig. 3, Table 2). The introduced irises appeared unaffected by intraspecific or interspecific competition treatments, but native irises produced substantially less biomass when grown in the same container with introduced irises. There were several nonsignificant interactions: species × salinity ( $F_{2, 84} = 1.85, P = 0.16$ ), salinity × competition ( $F_{4, 84} = 0.7, P = 0.59$ ), and species × salinity × competition ( $F_{4, 84} = 0.24, P = 0.91$ ).

**Species and competition**—After growing in containers for 18 mo, the introduced irises produced substantially more biomass than the native species ( $F_{1, 95} = 78.0, P < 0.0001$ , Figs. 2, 4). Competition strongly reduced total biomass ( $F_{2, 95} = 7.3, P = 0.001$ , Table 2, Fig. 3), but the effect differed between iris species (competition × species interaction:  $F_{2, 95} = 6.7, P = 0.002$ , Fig. 3). The introduced iris was not affected by either intraspecific or interspecific competition and produced similar amounts of biomass in all competition treatments. In contrast, the native iris produced much less biomass in the interspecific competition treatment. In a few of the containers, the native irises were literally pushed out by aggressive growth of *I. pseudacorus* (Fig. 2).

**Salinity**—Salinity had a strong negative effect on biomass of both species ( $F_{2, 95} = 21.7, P < 0.0001$ , Table 3, Fig. 4). The introduced iris

**TABLE 1.** Strong positive correlations among response variables. Values shown are Pearson's correlation coefficients (*r*) for log-transformed data, with *P* values below (*N* = 100).

Variable	Ramet mass	Root mass	Leaf mass	No. of ramets
Ramet mass	1.0	0.64	0.85	0.55
Root mass		1.0	0.61	0.78
Leaf mass			1.0	0.47
No. of ramets				1.0

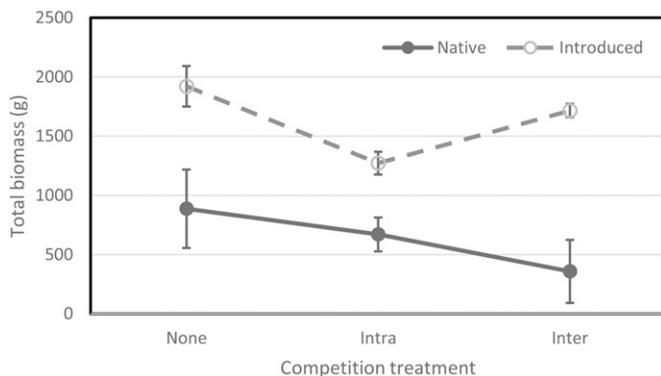


**FIGURE 2** Belowground biomass of introduced *Iris pseudacorus* (above) and native *I. hexagona* (below) grown in an interspecific competition treatment for 18 mo. Biomass of the introduced iris was approximately 120 cm in diameter. Photo by Karen Wiens.

produced more biomass than the native iris in both salinity treatments, but the difference was not significant (species  $\times$  salinity interaction =  $F_{2,84} = 1.85$ ,  $P = 0.16$ ).

## DISCUSSION

Wetlands encompass about 6% of the Earth's surface (Mitsch and Gosselink, 1993) but harbor 24% of the world's destructive, invasive plants (Zedler and Kercher, 2004; Stephens and Sutherland, 1999; With, 2002). As sea levels rise with changing global climate, wetlands will become even more salinized (Michener et al., 1997; Sánchez Sánchez and Islebe, 1999; Goldenberg et al., 2001). Such



**FIGURE 3** The effects of species and competition on total biomass. There were significant species, competition and species  $\times$  competition effects. Means  $\pm$  SE in grams are displayed in an interaction plot to better illustrate the main effects and their interactions (SAS, Linear Models, Plots).

disturbances can create unoccupied niches if native inhabitants experience heavy mortality, and thus provide opportunities for exotic colonists (Davis et al., 2000; Brown and Mitchell, 2001; Marvier et al., 2004). That some species reach high population densities as they invade novel, disturbed habitats, yet remain at low densities in their native range, is a paradox that despite copious research, is unresolved (Daehler et al., 2004; Davis et al., 2006; Meiners, 2007; Van Kleunen and Johnson, 2007; Pathikonda et al., 2008; Rout and Callaway, 2009).

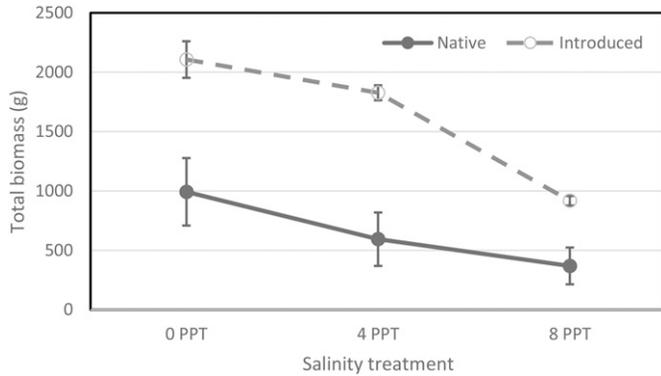
Based on our previous quantitative models that simulated long-term population dynamics of *I. hexagona* and *I. pseudacorus* (Pathikonda et al., 2008), we predicted the introduced iris would eventually exclude native irises from freshwater wetlands, but the native iris would coexist with or exclude introduced irises in intermediate-brackish salinity marsh. Our original models were parameterized using results from extensive field and experimental studies of the native iris (e.g., Van Zandt and Mopper, 2002; Van Zandt et al., 2003), combined with an unpublished pilot experiment comparing growth of the introduced and native irises in different salinity

treatments. Unexpectedly, in the current experiment, *I. pseudacorus* produced substantially more biomass than *I. hexagona* in freshwater and salinity treatments, and was unaffected by interspecific competition. Unlike the native, the introduced iris produced roughly the same amount of biomass in all three competition treatments. (Figs. 3, 4). Both native and introduced irises allocated about 99% of their total biomass to belowground clonal ramets and roots, but the introduced species rapidly occupied available mesocosm space, especially in the freshwater treatment, leaving little room for growth of the native.

Both species were negatively affected by salt and produced half as much biomass in the high salinity treatment as in freshwater (Table 3, Fig. 4). The salinity treatments in our experiment represent typical levels in Louisiana coastal marsh, although severe salt spikes occur (Michener et al., 1997; Mulholland et al., 1997; Burkett and Kusler, 2000; Van Zandt and Mopper, 2002). Many plant populations were killed in 2005 by Hurricane Rita because saltwater inundated freshwater wetlands (Guidroz et al., 2007). Such forces can devastate ecological communities, leaving them vulnerable to invasion by introduced plants and animals (Vitousek, 1994; With,

**TABLE 2.** The effects of species (*Iris hexagona* (native) and *I. pseudacorus* (introduced)) and competition (none, intraspecific (intra), interspecific (inter)) on total biomass. Values shown are the  $P$ -values determined by Tukey-adjusted pairwise comparisons of data shown in Fig. 3.

Treatment	Native, intra	Native, inter	Introduced, none	Introduced, intra	Introduced, inter
Native, none	0.732	0.0001	0.012	0.25	0.04
Native, intra		0.006	0.0001	0.004	0.0002
Native, inter			0.0001	0.0001	0.0001
Introduced, none				0.76	0.996
Introduced, intra					0.96



**FIGURE 4** The effects of species and salinity on total biomass. Both species and salinity had significant effects on total biomass but the species × salinity effect was not significant. Means ± SE are displayed in an interaction plot to better illustrate the main effects and their interactions (SAS, Linear Models, Plots).

2002). Slight amounts of salt cause severe physiological stress in freshwater plants (Hasegawa et al., 2000; Xiong and Zhu, 2002) because energy must be allocated to process Na<sup>+</sup> ions and to synthesize the osmolytes that balance water potential (Wang et al., 2008). Even among *I. hexagona* populations that are adapted to salinity (Pathikonda et al., 2010; Meerow et al., 2011), NaCl as low as 4 ppt can significantly affect endogenous hormones (Wang et al., 2001), reproductive mode (Van Zandt et al., 2003), flowering phenology (Van Zandt and Mopper, 2002), leaf senescence (Schile and Mopper, 2006), seed germination (Van Zandt and Mopper, 2004), florivory (Geddes and Mopper, 2006; Tobler et al., 2006), and herbivory (Wang and Mopper, 2008).

Although *Iris pseudacorus* outgrew the native iris in our experiment, it has not yet spread into the intermediate-brackish salinity native iris populations along the Louisiana Gulf Coast (Wiens, 2009). The combination of life-history traits and abiotic disturbance can complicate competition between native and introduced plants (Williamson and Fitter, 1996; Davis et al., 2000) because their interactions are so heavily context-dependent (Ridenour and Callaway, 2001; Čuda et al., 2015; Zheng et al., 2015). Furthermore, clonal species like the irises we studied can adjust to competition, environmental disturbance, or optimize energetic resources by switching between sexual and clonal reproductive strategies (Loehle, 1987; Cheplick and Chui, 2001; Van Kleunen et al., 2001; Jongejans et al., 2006).

Using clonal growth as an assay, our results indicate that the introduced iris is more salt-tolerant than we predicted, and may eventually eradicate native irises in intermediate-brackish coastal wetlands. We know a lot about how salinity affects seed production

**TABLE 3.** The effects of species (*Iris hexagona* (native) and *I. pseudacorus* (introduced)) and salinity (0, 4, 8 parts per thousand) on total biomass (g). Values shown are the *P* values determined by Tukey-adjusted pairwise comparisons of data shown in Fig. 4.

Treatment	Native, 0	Native, 4	Native, 8	Introduced, 0	Introduced, 4	Introduced, 8
Native, 0	0.357	0.0009	0.001	0.0046	0.999	
Native, 4		0.242	0.0001	0.0001	0.585	
Native, 8			0.0001	0.0001	0.0036	
Introduced, 0				0.998	0.0005	
Introduced, 4					0.0023	

and survival in the native iris (Van Zandt and Mopper, 2002, 2004; Van Zandt et al., 2003), but much less is understood about the introduced iris. The information presented here on clonal growth advances our knowledge about how the environment affects interactions between native and introduced species, but we need to include the effects of salinity on sexual reproduction in the introduced iris to achieve a better understanding of the long-term population dynamics of wetland plant communities.

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**LITERATURE CITED**

Bennett, B. D., and J. B. Grace. 1990. Shade tolerance and its effect on the segregation of two species of Louisiana iris and their hybrids. *American Journal of Botany* 77: 100–107.

Brown, B., and R. Mitchell. 2001. Competition for pollination: Effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129: 43–49.

Burkett, V., and J. Kusler. 2000. Climate change: Potential impacts and interactions in wetlands of the United States. *Journal of the American Water Resources Association* 36: 313–320.

Carlton, C., V. Townsend Jr., P. Van Zandt, and S. Mopper. 2000. Description of the larvae of *Loberus impressus* Leconte with notes on its natural history (Languriidae: Xenoscelinae). *Annals of the Entomological Society of America* 93: 356–361.

Cheplick, G. P., and T. Chui. 2001. Effects of competitive stress on vegetative growth, storage and regrowth after defoliation in *Phleum pratense*. *Oikos* 95: 291–299.

Chmura, D., and E. Sierka. 2007. The invasibility of deciduous forest communities after disturbance: A case study of *Carex brizoides* and *Impatiens parviflora* invasion. *Forest Ecology and Management* 242: 487–495.

Cody, W. J. 1961. *Iris pseudacorus* escaped from cultivation in Canada. *Canadian Field Naturalist* 75: 139–142.

Coops, H., and G. Vanderveelde. 1995. Seed dispersal, germination and seedling growth of 6 helophyte species in relation to water level zonation. *Freshwater Biology* 34: 13–20.

Crawford, H. 2000. Connecticut Invasive Plant Working Group fact sheet: Yellow flag or European yellow iris: *Iris pseudacorus*. [http://www.hort.uconn.edu/cipwg/pdfs/yellow\\_flag.pdf](http://www.hort.uconn.edu/cipwg/pdfs/yellow_flag.pdf). University of Connecticut, Storrs, Connecticut, USA.

Čuda, J., H. Skálová, Z. Janovský, and P. Pyšek. 2015. Competition among native and invasive *Impatiens* species: The roles of environmental factors, population density and life stage. *AoB PLANTS* 7: plv033.

Daehler, C., J. Denslow, S. Ansari, and H. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific islands. *Conservation Biology* 18: 360–368.

Davis, M., J. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* 88: 528–534.

Davis, S. A., A. D. Landis, V. Nuzzo, B. Blossey, E. Gerber, and L. H. Hinz. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). *Ecological Applications* 16: 2399–2410.

- Dymes, T. A. 1920. Notes on the life history of *Iris pseudacorus*, Linn., with special reference to its seeds and seedlings. *Proceedings of the Linnean Society of London* 132: 59–63.
- García-Serrana, H., F. X. Sans, and J. Escarre. 2007. Interspecific competition between alien and native congeneric species. *International Journal of Ecology* 31: 69–78.
- Geddes, N., and S. Mopper. 2006. Effects of environmental salinity on vertebrate florivory and wetland communities. *Natural Areas Journal* 26: 31–37.
- Goldenberg, S. B., W. L. Christopher, M. Alberto, and W. Gray. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. *Science* 293: 474–479.
- Guidroz, W.S., W. S. Gregory, and D. Dane. 2007. Sediment transport along the Southwestern Louisiana shoreline: Impact from hurricane Rita, 2005. Coastal Sediments, American Society of Civil Engineers (New Orleans, Louisiana), 1–10.
- Hasegawa, P., R. Bressan, J. Zhu, and H. Bohnert. 2000. Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology* 51: 463–499.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Jongejans, E., H. De Kroon, and F. Berendse. 2006. The interplay between shifts in biomass allocation and costs of reproduction in four grassland perennials under simulated successional change. *Oecologia* 147: 369–378.
- Keane, R., and M. Crawley. 2002. Exotic plant invasions and enemy release hypothesis. *Trends in Ecology & Evolution* 17: 164–170.
- Lake, J. C., and M. R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: The role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215–226.
- Leger, E. A. 2008. The adaptive value of remnant native plants in invaded communities: An example from the Great Basin. *Ecological Applications* 18: 1226–1235.
- Loehle, C. 1987. Partitioning of reproductive effort in clonal plants: A benefit cost model. *Oikos* 49: 199–208.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invisibility. *Ecology* 80: 1522–1536.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.
- Marvier, M., P. Kareiva, and M. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multi-species metapopulation. *Risk Analysis* 24: 869–878.
- Meerow, A. W., M. Gideon, D. Kuhn, S. Mopper, and K. Nakamura. 2011. The genetic mosaic of iris series *Hexagonae* in Florida: Inferences on the Holocene history of the Louisiana irises and anthropogenic effects on their distribution. *International Journal of Plant Sciences* 172: 1026–1052.
- Mehrhoff, L. J., J. A. Silander Jr., S. A. Leicht, E. S. Mosher, and N. M. Tabak. 2003. Invasive plant atlas of New England: *Iris pseudacorus*. [www.invasive.org/weedcd/pdfs/ipane/Irispseudacorus.pdf](http://www.invasive.org/weedcd/pdfs/ipane/Irispseudacorus.pdf).
- Meiners, S. J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88: 1098–1104.
- Michener, W. K., E. R. Blood, K. L. Bildstein, M. M. Brinson, and L. R. Gardener. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770–801.
- Mitsch, W., and J. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, New York, USA.
- Mopper, S., Y. Wang, C. Criner, and K. Hasenstein. 2004. *Iris hexagona* hormonal response to salinity stress, leafminer herbivory, and phenology. *Ecology* 85: 38–47.
- Mulholland, P. J., G. R. Best, C. C. Coutant, G. M. Hornberger, J. L. Meyer, P. J. Robinson, J. R. Stenberg, et al. 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. *Hydrological Processes* 11: 949–970.
- Pathikonda, S., A. S. Ackleh, K. H. Hasenstein, and S. Mopper. 2008. Invasion, disturbance, and competition: Modeling the fate of coastal plant populations. *Conservation Biology* 23: 164–173.
- Pathikonda, S., A. Meerow, Z. He, and S. Mopper. 2010. Salinity tolerance and genetic variability in freshwater and brackish *Iris hexagona* colonies. *American Journal of Botany* 97: 1438–1443.
- Preece, S. J. 1964. *Iris pseudacorus* in Montana. *Proceedings of the Montana Academy of Sciences* 24: 1–4.
- Raven, P. H., and J. H. Thomas. 1970. *Iris pseudacorus* in western North America. *Madroño* 20: 390–391.
- Ridenour, W. M., and R. M. Callaway. 2001. The relative importance of allelopathy in interference: The effects of an invasive weed on a native bunchgrass. *Oecologia* 126: 444–450.
- Rout, M., and R. M. Callaway. 2009. An invasive plant paradox. *Science* 324: 734–735.
- Sánchez Sánchez, O., and G. A. Islebe. 1999. Hurricane Gilbert and structural changes in a tropical forest in south-eastern Mexico. *Global Ecology and Biogeography Letters* 8: 29–38.
- SAS. 2015. Statistical Analysis Software, Enterprise Guide, version 7.11. SAS Institute, Cary, North Carolina, USA.
- Schile, L., and S. Mopper. 2006. Negative effects of salinity stress on a leaf-mining insect and its host plant. *Ecological Entomology* 31: 1–7.
- Simberloff, D. 2000. Global climate change and invasive species in United States Forests. *Science of the Total Environment* 262: 253–261.
- Stephens, P., and W. Sutherland. 1999. Consequences of the Allee effect for behavior, ecology and conservation. *Trends in Ecology & Evolution* 14: 401–405.
- Sutherland, W. J. 1990. Biological flora of the British Isles: *Iris pseudacorus* L. no. 169. *Journal of Ecology* 78: 833–848.
- Sutherland, W. J., and D. Walton. 1990. The changes in morphology and demography of *Iris pseudacorus* L. at different heights on a saltmarsh. *Functional Ecology* 4: 655–659.
- Taylor, C., H. Davis, J. Cuvillier, F. Grevstad, and A. Hastings. 2004. Consequences of an allee effect in the invasion of a Pacific estuary by *Spartina alterniflora*. *Ecology* 85: 3254–3266.
- Thomas, L. K. 1980. The impact of three exotic plant species on a Potomac Island. National Park Service Scientific Monograph Series, no. 13. U. S. Department of the Interior, Washington, D. C., USA.
- Tobler, M., P. Van Zandt, K. Hasenstein, and S. Mopper. 2006. Growth and reproduction of a clonal plant in response to salinity and florivory. *Wetlands* 26: 803–812.
- USDA NRCS. 2002. The PLANTS Database, version 3.5. Available at <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, Louisiana, USA [accessed April 2005].
- Van Kleunen, M., M. Fischer, and B. Schmid. 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos* 94: 515–524.
- Van Kleunen, M., and S. G. Johnson. 2007. South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions. *Journal of Ecology* 95: 674–681.
- Van Zandt, P. A., and S. Mopper. 2002. Delayed and carryover effects of salinity on flowering in *Iris hexagona* (Iridaceae). *American Journal of Botany* 89: 364–383.
- Van Zandt, P. A., and S. Mopper. 2004. Effects of maternal salinity and seed environment on germination and growth in *Iris hexagona*. *Evolutionary Ecology Research* 6: 813–832.
- Van Zandt, P. A., M. A. Tobler, E. Mouton, K. H. Hasenstein, and S. Mopper. 2003. Positive and negative consequences of salinity stress for the growth and reproduction of the clonal plant, *Iris hexagona*. *Journal of Ecology* 91: 837–846.
- Vitousek, P. M. 1994. Biological invasions and ecosystem properties, can species make a difference? In H. A. Mooney and J. A. Drake [eds.], *Ecology of biological invasions of North America and Hawaii*, 163–173. Springer-Verlag, New York, New York, USA.
- Wang, H. G., and S. Mopper. 2008. Separate and interacting effects of deer florivory and salinity stress on iris herbivores. *Oikos* 117: 564–570.
- Wang, Y., S. Mopper, and K. Hasenstein. 2001. Effects of salinity on endogenous levels of ABA, IAA, JA, and SA in *Iris hexagona*. *Journal of Chemical Ecology* 27: 327–342.
- Wang, Y., S. Mopper, and K. H. Hasenstein. 2008. Osmolytes in salinity-stressed *Iris hexagona*. *Acta Physiologiae Plantarum* 30: 715–721.

- Wiens, K. C. 2009. Invasion front or range boundary? Factors limiting invasive species. Dissertation. University of Louisiana, Lafayette, Louisiana, USA.
- Williamson, M. H., and A. Fitter. 1996. The characters of successful invaders. *Biological Conservation* 78: 163–170.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conservation Biology* 16: 1192–1203.
- Xiong, L., and J. Zhu. 2002. Salt tolerance. *The Arabidopsis Book* 1: e0048.
- Zedler, J., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists and outcomes. *Critical Reviews in Plant Sciences* 23: 431–452.
- Zheng, Y., Y. Zheng, Y. Feng, A. Valiente-Banuet, Y. Li, Z. Liao, J. Zhang, and Y. Chen. 2015. Are invasive plants more competitive than native conspecifics? Patterns vary with competitors. *Scientific Reports* 5: 15622; doi: 10.1038/srep15622.