

DELAYED AND CARRYOVER EFFECTS OF SALINITY ON FLOWERING IN *IRIS HEXAGONA* (IRIDACEAE)¹

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Saltwater intrusion into wetland ecosystems has destroyed or damaged many native plant populations. *Iris hexagona* is a salt-sensitive species that exhibits intraspecific variation in salinity tolerance. To investigate the effect of salinity on flowering, we exposed *I. hexagona* collected from natural populations to salt treatments in a common garden. Experimental salinity additions strongly delayed flowering phenology, but the effect was not apparent until the second year, when less than 4 g/L NaCl delayed flowering up to 3 d. In the field, soil salinity and flowering phenology varied substantially within *I. hexagona* populations. Iris flowers are receptive to pollinators for 2 d or less, therefore a 3-d delay could affect outcrossing dynamics, and ultimately, the evolutionary ecology of iris populations. Salinity also had a carryover effect; prior salinity exposure delayed flowering in irises that had been replanted in freshwater conditions for 6 mo. This is an important result because it suggests that episodic stress (such as tropical storms) can influence performance well after the stress has disappeared. Our research further underscores the importance of long-term studies because a 1-yr experiment would have failed to reveal the strong effects of salinity that emerged in the second year.

Key words: flowering phenology; freshwater wetlands; glycophyte; phytohormones; salinity stress.

Flowering is a life history trait determined by plant genotype, the environment, and the interaction between them (Rathcke and Lacey, 1985). The timing of flower production can be critical for the evolutionary ecology of plant populations (Augspurger, 1981; Fox, 1990b). Synchronized flowering can increase the effective population size, reduce genetic structure, and maximize outcrossing (Augspurger, 1981; Primack, 1985). In contrast, asynchronous flowering can impede gene flow (Primack, 1985; Cruzan et al., 1994) and reduce reproductive success (Rathcke and Lacey, 1985; Fox, 1990a). In addition to genetic mechanisms, flowering is also affected by environmental factors such as photoperiod (Shitaka and Hirose, 1998), temperature (Price and Waser, 1998; Sandvik and Totland, 2000), herbivory (Jackson, 1966; Marquis, 1988; English-Loeb and Karban, 1992; Pilon, 2000), and water stress (Fox, 1990a, 2001; Kelly, 1992; Bram and Quinn, 2000; Stanton, Roy, and Theide, 2000).

Wetland plants are heavily impacted by saltwater intrusion, which can destroy or damage sensitive populations (Pezeshki, DeLaune, and Patrick, 1990; Krauss et al., 2000). However, some wetland species exhibit intraspecific variation in salinity tolerance, and it is particularly important to understand the effects of salinity on plants that can survive saline conditions (Allen, Chambers, and Pezeshki, 1997; Hester, Mendelssohn, and McKee, 1998; Seliskar and Gallagher, 2000). *Iris hexagona* (Walter) is indigenous to coastal wetlands and has be-

come an important model for ecological and evolutionary research (Bennett and Grace, 1990; Arnold, Hamrick, and Bennett, 1993; Burke et al., 2000). This native Louisiana species occurs primarily in freshwater and brackish wetlands, and observations of these populations indicate that they exhibit high mortality due to saltwater intrusion. However, several populations inhabit brackish marsh environments, making *I. hexagona* a good species for studying ecological responses to environmental stress.

Salinity is a growing environmental concern in wetland communities (Twilley et al., 2001), but we know very little about how salt exposure affects flowering in natural plant populations. Drought stress has been observed to delay flowering (Fox, 1990a, 2001; Kelly, 1992; Bram and Quinn, 2000; Stanton, Roy, and Theide, 2000); since salinity and drought cause similar osmotic responses in plants (Levitt, 1980), we hypothesized that salinity should produce flowering delays. In Louisiana, salinity stress is often episodic because it results from tropical storms. Because clonal plants can retain the effects of previous environmental conditions for subsequent generations of ramets (Schwaegerle, McIntyre, and Swingle, 2000), we determined whether salinity had a carryover effect on floral phenology. We conducted common garden experiments to test these predictions and imposed two different salinity regimes on *I. hexagona* collected from natural populations: (1) continuous exposure to salinity and (2) salinity treatment followed by a return to freshwater conditions.

MATERIALS AND METHODS

Natural history—*Iris hexagona* Walter (Iridaceae) is a perennial species indigenous to freshwater marshes of the southern Atlantic and Gulf coasts and is widely distributed in Louisiana, USA (Viosca, 1935). Flowers appear from late March to late April and are pollinated by *Bombus* spp. (Caillet and Mertzweiler, 1988; Cruzan and Arnold, 1993). Flowers are very short-lived and are available to pollinators for a maximum of 2 d. *Iris hexagona* produces large seed capsules containing 40–60 seeds and also reproduces vegetatively through sympodial rhizomes. Salinity tolerant *I. hexagona* occur on Marsh Island, a 300-km² intermediate salt marsh located between the Vermilion Bay and the Gulf of Mexico, 10 km south of mainland Louisiana (29.79° N, 91.78° W).

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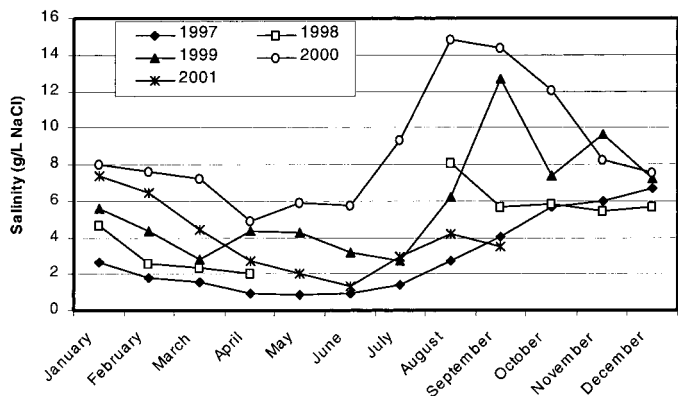


Fig. 1. Mean hourly salinity measurements taken at one of the iris sites on Marsh Island 10 km south of mainland Louisiana, USA, from 1997 to 2001. Data provided by Edmond Mouton, State of Louisiana Department of Wildlife and Fisheries.

Field salinity levels—To determine surface water salinity at Marsh Island, we used data obtained from hourly measurements conducted by The State of Louisiana Department of Wildlife and Fisheries (E. Mouton, State of Louisiana Department of Wildlife and Fisheries, personal communication) on a YSI model 30 SCT salinity meter (YSI, Yellow Springs, Ohio, USA). Data were averaged from hourly readings taken at four sites from 1997 to 2001. We also monitored soil interstitial salinity at our sites by inserting a probe to a depth of 20 cm, extracting soil water with a syringe, and measuring the sample with an Orion 125 conductivity meter (Orion Research, Beverly, Massachusetts, USA). To compare temporal and spatial variation, we measured surface water and interstitial soil salinity on 5 March 1999, 6 June 2000, and 26 September 2000 at four *I. hexagona* sites. At each site we obtained salinity levels at three locations on a 7-m transect from the bank, as well as the surface water adjacent to the bank.

The common garden—We conducted two experiments to investigate the effects of salinity on *I. hexagona* flowering phenology. In March 1997, we established a common garden at the University of Louisiana Center for Ecology and Environmental Technology (CEET) in Carencro, Louisiana. We collected plants from ten widely separated sites on Marsh Island and planted them in 30 227-L plastic tubs filled with Mississippi alluvial topsoil. Tubs were large enough to prevent crowding of irises. We used Instant Ocean (Aquarium Systems, Mentor, Ohio, USA), a nitrate- and phosphate-free synthetic sea salt, to establish and maintain salinity levels in the supplemental salinity tubs, and the soil was kept saturated throughout the experiment. Salinity levels were recorded weekly and adjusted as necessary to maintain salinity treatments.

Experiment 1—This experiment tested the effects of site of collection and 12 mo of continuous exposure to salinity on *I. hexagona* flower phenology. Ten tubs each were randomly assigned to a low, medium, or high salinity treatment (0.2 ± 0.4 g/L, 2.0 ± 1.2 g/L, and 3.7 ± 1.8 g/L salinity, respectively; means ± 1 SE). The treatment salinities reflected island surface water salinity levels in the months when irises flower (Fig. 1). Each tub contained random combinations of marked plants from three sites, and each site ($N = 10$) \times salinity ($N = 3$) combination was replicated three times. The low salinity tubs did not receive supplemental salt. Irises planted in the common garden in March 1997 flowered in April 1998. From 9 April until 26 April we monitored every flower produced and recorded the date of sepal opening. After flowering, plants remained in the salinity treatments until October 1998, when they were carefully excavated and placed in fresh water. Plants grew in fresh water for 2 mo and were then replanted into tubs for the second experiment.

Experiment 2—This experiment again examined the effect of salinity on flowering phenology and additionally determined if previous exposure to sa-

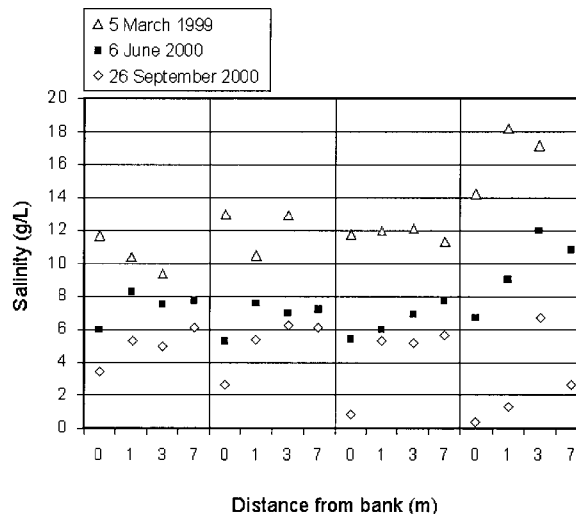


Fig. 2. Salinity readings at four sites (separated by vertical bars) at Marsh Island on three different dates. Surface water was sampled at the bank (0 m), while interstitial readings were taken at 1, 3, and 7 m inland at a depth of 20 cm.

linity affected flowering in plants that were no longer experiencing saline conditions. To examine these questions, we established 15 low and 15 high salinity treatments (0.5 ± 0.05 g/L and 3.0 ± 0.18 g/L, respectively) in the original 30 tubs using fresh soil and randomly selected a subset of the excavated irises for replanting. Low and high salinity irises from the 1998 experiment were replanted into similar low and high salinity treatments in the 1999 experiment. The medium salinity plants from the first experiment were randomly assigned to either a low or high salinity treatment in the second experiment. Therefore, experiment 2 consisted of four salinity treatments: (1) low salinity in 1998 and 1999 (low); (2) medium salinity in 1998 and low salinity in 1999 (medlow); (3) medium salinity 1998 and high salinity in 1999 (medhigh); and (4) high salinity in 1998 and 1999 (high). We conducted this experiment from December 1998 until May 1999 and monitored flowering from 28 March to 6 May as in experiment 1. Plants from each site were represented equally in both the medlow and medhigh treatments.

Data analysis—To examine the differences in flowering phenology, we used survival analysis with a Cox regression model, which conducts a chi-square test with one degree of freedom (SAS PROC PHREG, version 8.2; SAS Institute, 2001). Effects of both salinity and collection site were included in the analyses. Survival analysis is commonly used for survival (Allison, 1995; Hardin, Willers, and Wagner, 1996), flowering (Fox, 1990a,b, 2001), germination (Platenkamp and Shaw, 1993; Fox, 2001), and pollination data (Muenchow, 1986). We employed the COVSANDWICH option of PHREG because it generates robust standard errors for nonindependent observations (Lee, Wei, and Amato, 1992), such as flowers produced by a single stalk.

RESULTS

Field salinity levels—Water salinities vary monthly on Marsh Island in a consistent pattern. Water salinity data from one iris site are presented to illustrate temporal variation (Fig. 1). Salinity is lowest in the spring, averaging 2.8 ± 0.3 g/L in April when irises flower. The highest levels occur from August to November and average 8.0 ± 0.5 g/L. Interstitial soil salinity is higher than water salinity and also varies considerably (Fig. 2). Temporal and spatial variation within the 7-m site transects exceeded variation between the sites, which were separated by 1–5 km. Similar to water salinity, the lowest soil salinity occurs in the spring, which is the time of flowering for *I. hexagona*. The annual rise in salinity from 1997 to 2000

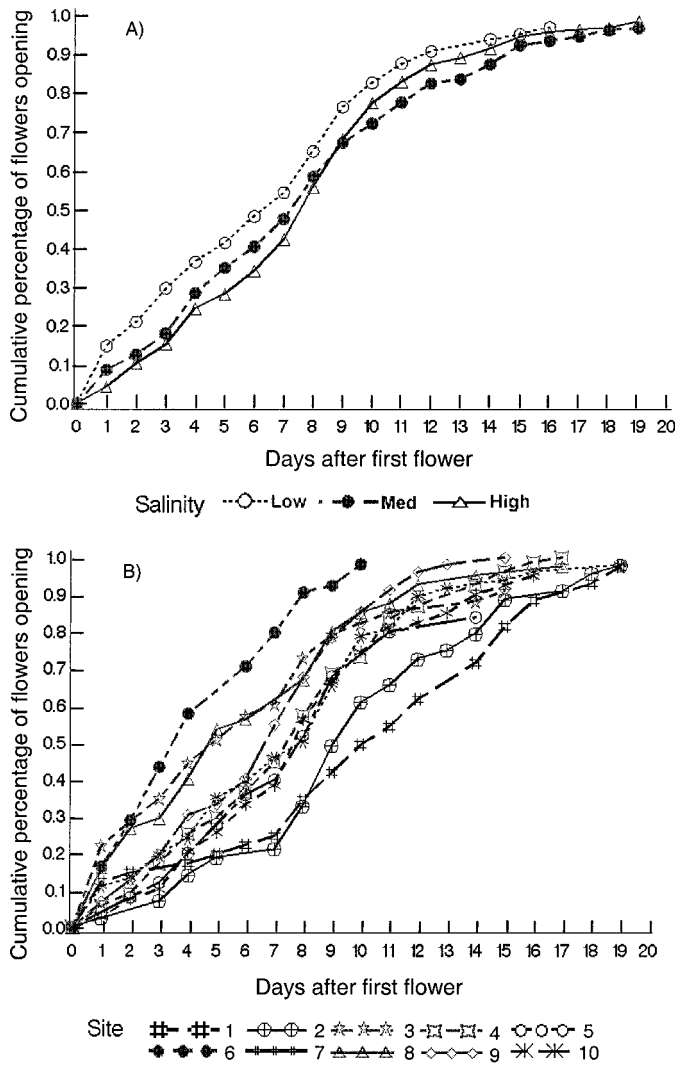


Fig. 3. Effect of salinity (A) and collection site (B) on flowering phenology in experiment 1.

coincided with a drought in southern Louisiana, which ended in 2001.

Flowering phenology—The first 12 mo of exposure to salinity did not significantly alter flower phenology in experiment 1 ($\chi^2 = 1.43, P = 0.23, df = 1$; high vs. low $\chi^2 = 1.55, P = 0.21, df = 1$; Fig. 3A). While flowering responses in plants collected from different sites were highly variable (maximum difference of 7 d; compare sites 6 and 7 in Fig. 3B), the ten sites did not differ significantly in the timing of flower production ($\chi^2 = 2.15, P = 0.14, df = 1$).

A stronger effect of salinity in delaying flowering emerged in experiment 2 ($\chi^2 = 5.22, P = 0.02, df = 1$), where median flowering dates differed by as much as 3 d and the rate of flower opening was faster in lower salinities (Fig. 4). The delay in flowering phenology between the low and high groups was significant during this year ($\chi^2 = 5.12, P = 0.024, df = 1$, sequential Bonferroni $\alpha = 0.025$) and was in the same direction as the low and high treatments in experiment 1. A significant carryover effect is indicated by plants in the med-low treatment flowering later than plants in the low treatment

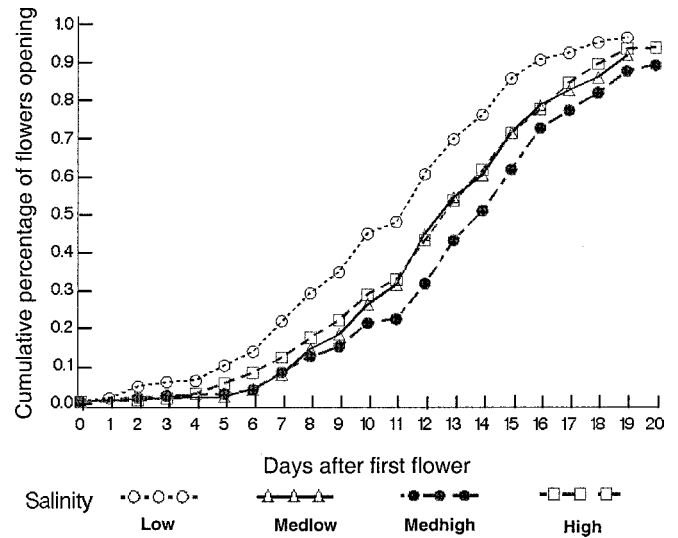


Fig. 4. Delayed and carryover effects of salinity exposure on flowering phenology in experiment 2. Treatments are as follows: Low = low salinity in 1998 and 1999, Medlow = medium salinity in 1998 and low salinity in 1999, Medhigh = medium salinity in 1998 and high salinity in 1999, and High = high salinity in 1998 and 1999.

($\chi^2 = 5.80, P = 0.016, df = 1$, sequential Bonferroni $\alpha = 0.017$), suggesting that the saline environment of the previous year still affected plants in the medlow treatment. There was no significant delay between the high and medhigh salinity treatments ($\chi^2 = 0.9, P = 0.34, df = 1$, sequential Bonferroni $\alpha = 0.05$). As in experiment 1, plants from different sites did not differ in their pattern of flower production ($\chi^2 = 0.27, P = 0.60, df = 1$).

DISCUSSION

Although other researchers have observed a delay in flowering with increased salinity levels (Blits and Gallagher, 1991; Stanton, Roy, and Theide, 2000), this is the first study we know of that experimentally tests the effect of salinity on the flowering phenology of a native wetland species. *Iris hexagona* is salt-sensitive but exhibits intraspecific variation in tolerance, as indicated by observations of mainland freshwater populations that exhibited drastic dieback due to storm-derived saltwater intrusion. Our study demonstrates that relatively low levels of salinity can delay flowering by as much as 3 d (Fig. 4). Salinity-induced flowering delays have been observed in wild mustard (*Sinapis arvensis*), an annual, non-wetland, salt-sensitive species (Stanton, Roy, and Theide, 2000), as well as in the salt-tolerant marsh species *Cakile edentula* (Boyd and Barbour, 1986) and *Sporobolus virginicus* (Blits and Gallagher, 1991). Although little is known about how salinity stress shapes life history evolution of natural populations of glycophytes, there is some evidence that it can enhance evolutionary potential and genetic diversity (Stanton, Roy, and Theide, 2000). This is certainly possible in *I. hexagona*, which, despite delayed flowering, produces significantly more seeds when exposed to increased salinity (Van Zandt, 2001).

The impact of salinity stress—The effect of salinity on *I. hexagona* flowering phenology was both delayed and persistent. Although a significant salinity effect did not appear until the second year (experiment 2) of exposure (Fig. 4), the effects

persisted in plants returned to freshwater conditions for 6 mo (the medlow group in experiment 2). This observation has particular relevance for coastal populations that typically experience wide variation in salinity (Adam, 1990). Fluctuations in salinity can create windows of opportunity for sensitive developmental stages such as seeds (Houle et al., 2001), but our study suggests that mature plants retain the effects of salinity even during periods of low stress.

A carryover effect on phenology could explain the lack of significant treatment differences in experiment 1. Since all plants were collected from saline environments, their phenological responses in the first experiment may have been more strongly influenced by natural site salinity than experimental salinity. Such a carryover effect was observed in the clonal sedge *Eriophorum vaginatum*, in which growth and clonal propagation were influenced by the parental environment, independent of plant mass (Schwaegerle, McIntyre, and Swingley, 2000). Our study extends this observation by revealing that prior exposure to environmental stress can affect sexual traits of clonal plants. It also demonstrates the value of long-term experiments when examining performance in perennial plants, as a 1-yr experiment would have failed to reveal the strong *I. hexagona* responses to salinity that appeared in the second year.

Mechanisms of delayed phenology—Because salinity exerts multiple stresses on plants, including osmotic imbalance, nutritional deficits, and cellular toxicity (reviewed in Levitt, 1980; Wang, Mopper, and Hasenstein, 2001), it may be difficult to identify the specific mechanisms that alter life history shifts in important traits such as flowering phenology. One potentially important factor facilitating delayed flowering in *I. hexagona* could be reduced belowground biomass. Excavation of all common garden plants in October 1998 revealed that salinity-treated plants had a 30% reduction in belowground biomass compared to plants grown in low salinity (Van Zandt, 2001). A reduction in energetic reserves of this magnitude could impede the development of floral structures and delay anthesis. However, salinity did not have a negative effect on the total number of flowers produced, and while plant biomass was positively correlated with flower number, it was not a strong predictor of flower production ($r^2 = 0.01\text{--}0.14$; Van Zandt, 2001).

Phytochemical analyses of irises in our common garden indicated that salinity strongly alters the concentration of hormones in flower stalks and other plant tissues (Wang, Mopper, and Hasenstein, 2001). Both abscisic acid (ABA) and jasmonic acid (JA) were up-regulated in irises exposed to salinity (Wang, Mopper, and Hasenstein, 2001). Jasmonic acid moderates the effects of salinity (Moons et al., 1997) and osmotic stress (Creelman and Mullet, 1995; Finch-Savage, Blake, and Clay, 1996), as well as controls the opening of florets in rice (Zeng et al., 1999). Similarly, ABA induces genes involved in osmotic stress protection (Serrano and Gaxiola, 1994) and inhibits germination (Skriver and Mundy, 1990; Baskin and Baskin, 1998). Because these hormones are induced by salinity in *I. hexagona* and have known stress and reproductive functions, they may enable iris to flower despite the salinity stress, albeit with a slight delay. The increased seed production observed in the high salinity group (P. A. Van Zandt et al., unpublished manuscript) could also be a response to the elevated JA.

Consequences for individuals and populations—In the common garden experiment, small differences in salinity caused flowering asynchrony of several days. There is sufficient variation in soil salinity within natural *I. hexagona* populations (Fig. 2) to result in similar phenological delays. In fact, during the 19 April salinity measurement, individual irises at different sites displayed a mixture of reproductive stages, ranging from flower buds to newly opened flowers to developing seed capsules. Because flowering in *I. hexagona* coincides with seasonal lows in salinity (Fig. 1), phenological differences within sites may exceed differences between sites.

The timing of sexual reproduction is a critical component of plant life history that affects fitness (Schemske, 1977; Marquis, 1988), species interactions (Augspurger, 1981; Evans, Smith, and Gendron, 1989; English-Loeb and Karban, 1992), and evolution (Primack, 1985; Fox, 1990b; O'Neil, 1997). In freshwater *I. hexagona* populations that exhibit natural variation in flower availability, a greater number of available flowers was shown to increase outcrossing rates (Cruzan et al., 1994). Since *I. hexagona* flowers are receptive to pollinators for 2 d or less (P. A. Van Zandt, unpublished data), a 3-d delay in flowering could eliminate gene flow between asynchronous plants. The levels of asynchrony produced by small differences in salinity could not only impact recombination opportunities, it could determine the effective size of the entire population. However, the importance of the salinity-mediated carryover effect demonstrated in this study could also moderate this effect.

Theory predicts that plant genotype and the environment determine patterns of sexual reproduction (Rathcke and Lacey, 1985), but environmental forces can override genetic traits (Fox, 1990a; Kelly, 1992), even when selection for synchrony is strong (Augspurger, 1981; O'Neil, 1997). Consistent variation in salinity among sites would amplify existing genetic variation among isolated *I. hexagona* and further subdivide the populations genetically (Stanton, Galen, and Shore, 1997). However, there is equal or greater variation in salinity within salt-marsh sites than between sites separated by substantial distance. Salinity appears to prevent reproductive synchrony among plants growing in proximity, which should promote genetic heterogeneity within iris populations and maintain genetic heterozygosity in stressful environments where adaptive plasticity is necessary for survival.

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