

GROWTH AND REPRODUCTION OF A CLONAL PLANT IN RESPONSE TO SALINITY AND FLORIVORY

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Abstract: Salinity is increasing in wetland ecosystems, but the consequences for ecological communities are poorly understood. *Iris hexagona* is the only North American iris that survives in brackish marsh. Environmental salinity affects the physiology, growth, and reproduction of this glycophytic perennial, as well as plant-herbivore interactions. In brackish wetlands, 80% of iris flowers are consumed by white-tailed deer (*Odocoileus virginianus*), which rarely browse flowers in freshwater habitats. We investigated the effects of florivory and salinity on *I. hexagona* sexual and clonal reproduction. Irises that were protected from deer produced 20 times more mature seed capsules than unprotected plants. Experimental floral browsing increased both belowground clonal growth by 30% ($P = 0.0003$) and flower production the following year by 16% ($P = 0.112$). Iris populations differed significantly in clonal reproduction ($P = 0.004$), and interactions between salinity and population affected clonal ($P = 0.005$) and sexual ($P = 0.054$) output, suggesting that populations may be differentially adapted to environmental salinity. Brackish conditions can promote floral browsing and loss of sexual reproduction, but plants such as *I. hexagona* can compensate by allocating more resources to belowground clonal growth.

Key Words: biomass, browsing, wetland, compensation, deer, flowers, herbivory, *Iris hexagona*, *Odocoileus virginianus*, perennial, reproduction, plasticity, rhizome

INTRODUCTION

Wetlands support a large diversity of species relative to other ecosystems and contribute a variety of critical services, including nutrient cycling, flood mitigation, and seed dispersal (Rogers and McCarty 2000). Roughly 30 percent of the nation's vascular flora is contained by wetlands that encompass less than 5 percent of the land area (Mitsch and Gosselink 2000). Coastal wetlands are vulnerable to a multitude of natural and anthropogenic environmental disturbances (Turner 1997), including tropical storms, sea-level rise, erosion, and development (Boesch et al. 1994, Jackson et al. 1995, Williams et al. 2003). Disturbance promotes salinization, a major threat to freshwater ecosystems worldwide (Grace and Guntenspergen 1999).

In 2005, Category III Hurricanes Katrina and Rita caused historic flooding and salt intrusion into Louisiana wetlands and further compromised environmental recovery of these resilient yet fragile ecosystems. Salt incursion is a major threat to Louisiana wetlands and has caused heavy mortality of freshwater plant populations (Pezeshki et al. 1990, Allen et al. 1997). Salinity disrupts plant physiological processes (Levitt, 1980, Yeo, 1983, Hasegawa 2000), increases mortality (Krauss et al., 2000), and reduces biodiversity (Flynn et al. 1995, Holm and Sasser 2001). It alters normal plant functions (Hale and Orcutt 1987), such as growth (Van Zandt et al. 2003), floral traits (Kelly 1992, Delesalle and Mazer 1996, Stanton et al. 2000, Van Zandt and Mopper 2002), and fertility (Greenway and Munns 1980, Carroll et al. 2001).

Plant communities are shaped by biotic, as well as abiotic stress. For example, white-tailed deer (*Odocoileus virginianus* Boddaert) selectively browse many plant species, some of which are threatened and endangered (Miller et al. 1992, Anderson 1994, Hanley 1997). Deer also affect plant growth, community composition, and morphology (Russell, et al. 2001). Other vertebrates are equally destructive, such as nutria (*Myocastor coypus* Kerr), which are a major introduced pest and cause wide-spread loss to above- and below-ground biomass, alter distribution patterns, and reduce species diversity (Taylor and Grace 1995, Evers et al. 1998, Holm and Sasser 2001, Randall and Foote 2005).

Flowers comprise a much smaller portion than foliage of the total plant biomass consumed by herbivores (Krupnick and Weis 1999) but their loss has profound implications for plant fitness (Louda and Potvin 1995, Matter et al. 1999, Mothershead and Marquis 2000). Florivory reduces fruit production (Muenchow and Delesalle 1992, Cunningham 1995), decreases seedling dispersal and recruitment (Calvo-Irabien and Islas-Luna 1999), modifies genetic structure (Smith and Ludwig 1976), and shrinks biodiversity of floral associates, including pollinators (Krupnick et al. 1999). Invertebrate florivory is typically characterized by localized, partial damage to floral tissues, but vertebrate browsing can eliminate the entire reproductive potential of individual plants, with repercussions that cascade through populations and communities (Lowenberg 1997, Calvo-Irabien and Islas-Luna 1999, Rodrigues and Monteiro-Filho 2000, Kirby 2001, Geddes and Mopper 2006).

As in temperate forests, deer are abundant in coastal ecosystems, but virtually nothing is known about their interactions with marsh plant populations or how abiotic stress in wetland communities affects deer densities or impact. Salinity has been shown to influence the interactions between vertebrate and invertebrate herbivores and their halophyte (salt-loving) host plant species (Grace and Ford 1996, Pennings et al. 1998). Halophytes minimize salinity stress with adaptations that control and regulate salt uptake like succulence, excretion, or sequestration in specialized receptacles (Hale and Orcutt 1987). In contrast, glycophytic plants such as *Iris hexagona* (Walters) have no specialized mechanisms or structures to excrete salt, which accumulates in reproductive and vegetative tissues (Wang 2002), producing symptoms of stress even at low salt concentrations (Greenway and Munns 1980, Van Zandt et al. 2003). Numerous studies have investigated the physiological responses of freshwater plants to salinity (Levitt 1980,

Hasegawa et al. 2000), but little is understood about the ecological role that salt plays in plant-herbivore interactions in wetland communities.

Wetland plants often employ clonal reproduction (Mitsch and Gosselink 2000). Obligately sexual plants can compensate for florivory, but the responses are constrained by many factors, including the intensity, predictability, and timing of browsing (Lowenberg 1994). Clonal plants have complex life histories that require unique approaches when assessing the consequences of florivory (Sackville-Hamilton et al. 1987, Fagerstrom 1992). Effects of florivory on clonal plants have been largely unexplored, but the capacity for both sexual and asexual propagation imparts greater plasticity when compensation for damage is necessary (Gardner and Mangel 1999). For example, cattle browsing of *Yucca elata* (Engelm) inflorescences promotes below-ground clonal growth (Kerley et al. 1993), as does artificial clipping of *Helianthus tuberosus* (L.) flower buds (Westley 1993). A shift from sexual to asexual modes of reproduction can exert a stabilizing force on plant population densities, despite the short-term reduction in fecundity (Kingsolver 1986).

Iris hexagona is a common clonal glycophyte and a native Louisiana iris that inhabits coastal wetlands from Florida to Texas. It is the only North American iris we know that tolerates intermediate-brackish conditions, although an introduced iris (*I. pseudacorus* L.) has reportedly high salinity tolerance (Raven and Thomas 1970, Sutherland 1990). We have conducted common garden and greenhouse experiments using *I. hexagona* collected from natural marsh populations. Our results indicate that low levels of salinity decrease biomass, delay flowering, and increase seed production (Van Zandt and Mopper 2002, Van Zandt et al. 2003). Maternal exposure to up to $9 \mu\text{g g}^{-1}$ NaCl improves seed germination and survival (Van Zandt and Mopper 2004). Furthermore, salinity alters concentrations of four important phytohormones (Wang et al. 2001) and strongly affects interactions between *I. hexagona* and a leafmining insect (Schile and Mopper 2006).

One of the most interesting discoveries of our research is that most (> 80%) of the flowers produced by brackish marsh *I. hexagona* are heavily browsed by white-tailed deer. Deer selectively feed on flowers and rarely consume other plant tissues, which are reported to be toxic to vertebrates (Craighead et al. 1963, Cornell University Poisonous Plants Database 2001). Deer are the only vertebrates we have observed that feed on *I. hexagona*. In this study, we used a common garden experiment to examine the separate and combined effects of floral predation and salinity on flower production and

clonal growth. Study plants were collected from three natural populations, and we compared their responses to the experimental treatments. We also surveyed levels of deer florivory in brackish marsh *I. hexagona* populations to assess the impact of deer on sexual reproduction.

METHODS

Study Species and Sites

Iris hexagona Walter (Iridaceae) is a long-lived perennial that occurs throughout freshwater wetlands of the North American Gulf and Atlantic Coasts (Viosca 1935). Some populations of *I. hexagona* tolerate elevated salinity and occur in intermediate to brackish marsh (Van Zandt and Mopper 2002). Plants have ten to twenty erect basal leaves 40–100 cm long and 1–3 cm wide. In April, three to five large (15 cm dia) blue flowers are produced on tall (1.5 m) flower stalks. Seeds mature in the summer, and most germinate from four to twelve months afterwards. *Iris hexagona* is self-compatible but requires pollination by *Bombus* spp. bumblebees (Viosca 1935, Van Zandt and Mopper 2004). Vigorous clonal reproduction occurs via stout, branching rhizomes that eventually separate into independent genets.

We conducted field research at the 300-km² Marsh Island Wildlife Refuge in Louisiana, USA (29.79 N, 91.78 W). Hundreds of *I. hexagona* populations containing from 50–300 individuals are patchily distributed throughout this coastal island. Study populations were selected to be as spatially dispersed in the wetland as possible and were isolated from each other by 1–3 km. The brackish marsh was once a freshwater wetland that separated from the mainland during the past 5,000 years (Orton 1959, Törnqvist *et al.* 1996). The dominant marsh species (approximately 80%) are *Spartina patens* (Aiton) Muhl. (wire grass), *Schoenoplectus pungens* var. *pungens* (Vahl) Palla (three-corner grass), and *Juncus roemerianus* Scheele (needlegrass rush), but woody shrubs (e.g., *Baccharis halimifolia* L., *Iva frutescens* L.) and trees (e.g., *Celtis leavigata* Willd., *Acacia farnesiana* Willd) also occur along elevated spoil banks (Lindscombe *et al.* 1998).

Salinity is lowest during *I. hexagona* flowering in April, averaging 2.8 $\mu\text{g g}^{-1}$ (Van Zandt and Mopper 2002); levels vary more seasonally within years than spatially between populations. During an extended drought, salinity attained 18 $\mu\text{g g}^{-1}$ (1999) but typically ranges from 2 to 12 $\mu\text{g g}^{-1}$ and averages annually 5 $\mu\text{g g}^{-1}$. Mainland coastal marshes are

intermediate and vary temporally from 0.2–2.5 $\mu\text{g g}^{-1}$ (Geddes and Mopper 2006). Permanent populations of white-tailed deer are abundant throughout coastal Louisiana and attain high densities in coastal marsh habitats (Lindscombe *et al.* 1998).

Field Surveys and Exclosure Experiment

We surveyed rates of florivory in nine (1999) and eleven (2000) isolated *I. hexagona* populations using airboats to reach remote areas. We minimized the effects of the airboat on island iris populations by traveling within the numerous waterways and avoiding contact with the isolated populations. Deer browsing is readily identifiable by shorn inflorescence petioles on flower stalks, and deer have been photographed (with infrared camera) consuming *I. hexagona* flowers on Marsh Island (Geddes and Mopper 2006). We quantified rate of florivory as the proportion of browsed stalks relative to the total number available within each *I. hexagona* population.

We erected six deer exclosures in March 2000 to protect plants and test the impact of floral browsing on seed production. Two cages were placed 10 m apart in each of three randomly selected *I. hexagona* populations, separated by a minimum of 2 km. The circular cages measured 1.5 m in height by 1 m in diameter and were constructed of rubber-coated large-mesh wire with openings of approximately 5 cm that prevented deer, waterfowl, and nutria browsing but allowed pollinators, primarily bumble bees, access to flowers. We stabilized cages with 3-m high \times 2-cm diameter Polyvinylchloride (PVC) pipe anchored 1.5-m into the soil.

Iris hexagona begins to flower in April, and we visited the sites from April through June to census reproduction and florivory. We counted the number of flower stalks, flowers, and developing seed capsules inside cages and in the unprotected area of similar size adjacent to the cages. Data from cages within populations were averaged and compared with the adjacent uncaged plots using a paired t-test.

Effects of Florivory, Salinity, and Population

We established a common garden in September 1998 to test the effects of florivory, plant population, and salinity on clonal growth and sexual reproduction. The experiment was conducted at the University of Louisiana Center for Ecology and Environmental Technology (<http://ceet.louisiana.edu/>). We distributed 16, 227 L Rubbermaid™ containers in a 25 \times 15 m² research plot in open pasture and filled

them with commercially available Mississippi deltaic clay soil similar in composition and character to the Late Pleistocene soils that underlay Marsh Island (Orton 1959). We collected, weighed, and planted irises from three Marsh Island populations. The populations were selected because they produced significantly different amounts of biomass and flowers in a previous experiment (Van Zandt et al. 2003). Three plants from a single population were placed into an experimental container, and the mesocosms were randomly assigned to either a control (no supplemental salt, $n = 9$), or salinity treatment ($4.6 \pm 1.2 \mu\text{g g}^{-1}$, $n = 7$). Single plants typically contained from 6 to 12 leaves attached to a rhizome 15–35 cm long.

We used Instant Ocean™ synthetic sea salt (Aquarium Systems Inc., Mentor, Ohio, USA) to elevate soil salinity, which we monitored weekly with an Orion 125™ conductivity meter (Orion Research Inc., Beverly, MA), adjusting as necessary. Treatment salinity reflected natural levels at the Marsh Island study site (Van Zandt and Mopper 2002). For each container, one plant from the population was randomly assigned to the florivory treatment, and one plant was assigned to the control (no florivory) treatment. The third was planted in the event of transplant mortality, but none occurred. To ensure fertilization and capsule development in the controls, we hand-pollinated all flowers with pollen from non-experimental plants. Flowering began in early April 1999. To simulate vertebrate browsing and reduce potential artifacts from mechanical clipping (Baldwin 1990), the first author mimicked deer feeding by biting flowers from the petiole the first day of anthesis.

In August 1999, we collected, dried, counted, and weighed the mature flower stalks and seed capsules from the control irises. In late September 1999, we non-destructively excavated the control and treatment plants and measured total biomass (g), leaf area (cm^2), number of leaves, number of rhizomes, and rhizome size (volume). Rhizomes are cylinders and to estimate their size, we used the formula: $\text{length} \times ((\text{radius})^2) \cdot \pi$. We immediately replanted the irises so they would reproduce the following April. We used the correlation between *I. hexagona* leaf area and leaf mass to estimate above-ground foliage biomass ($r = 0.98$, $P < 0.0001$, Van Zandt et al. 2003). In the control group, we also added the sexual structures to the aboveground biomass estimate.

Statistical Analyses

To examine the effects of florivory and salinity on *I. hexagona* growth, we conducted a three-factor

multivariate analysis of variance (MANOVA). Florivory (no flowers browsed, all flowers browsed), salinity (control and saline), and iris population ($n = 3$) were fixed effects. The latter was fixed because we intentionally selected populations that had displayed significant differences in growth and reproduction in a previous experiment (Van Zandt et al. 2003). Of 16 total mesocosms, the number of population replicates within each salinity treatment was as follows: population 1—four control and three saline; population 2—three control and two saline; population 3—two control and two saline. Dependent variables were above-ground biomass, below-ground biomass, number of rhizomes, and rhizome size.

We used SAS Version 8.2 for all analyses (SAS Institute 2001). All variables met the normality and heteroscedasticity assumptions of ANOVA, except for the number of rhizomes, which we transformed using the Box-Cox macro in PROC UNIVARIATE. We first ran a saturated MANOVA (PROC GLM) with all variables and possible interactions, then removed the non-significant factors and variables and re-ran the analysis. To test if florivory influences future flower production, we used analysis of variance (PROC GLM) to compare the number of flowers produced in April 2000 by the plants that were experimentally browsed in April 1999. Non-transformed data are shown in all figures.

RESULTS

Field Surveys and Exclosure Experiment

Deer substantially reduced sexual reproduction of *I. hexagona* growing in brackish wetlands. Natural levels of deer florivory of Marsh Island irises averaged 81% in 1999 (± 11.4 SE, 9 populations) and 78% in 2000 (± 8.1 SE, 11 populations). Deer consumed entire flowers and some immature seed capsules, but rarely fed on foliage and avoided rhizomes altogether. The exclosure experiment indicates that such high levels of florivory can have a strong impact on *I. hexagona* fertility. Plants protected from florivory by deer exclosures produced 20-times more seed capsules than neighboring browsed irises (Figure 1; $t = 9.6$, $P = 0.005$, $df = 2$).

Effects of Florivory, Salinity, and Population

All response variables were positively correlated (except above- and below-ground biomass) in the experiment testing the effects of florivory, salinity, and population on *I. hexagona* growth (Table 1). Neither above-ground biomass nor number of

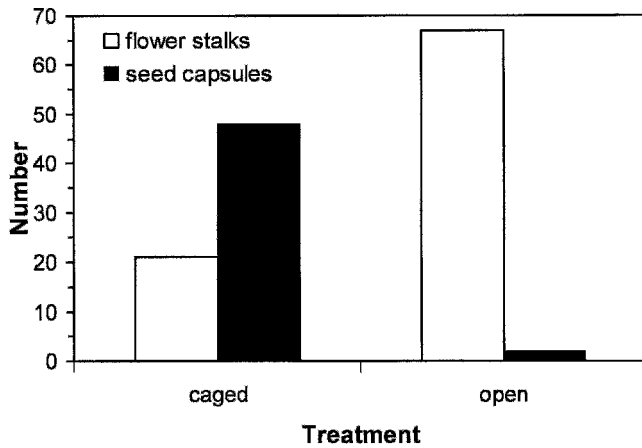


Figure 1. Total number of flower stalks and seed capsules produced by *I. hexagona* inside (caged) and outside (open) of deer exclosures in three natural *I. hexagona* populations.

rhizomes was influenced by the main effects, so we removed those dependent variables from the full model. There was no correlation between initial and final mass of plants (Pearson’s $r = 0.21$, $P = 0.16$); therefore, pre-treatment biomass was not included as a covariate. We also removed the non-significant interaction terms and re-ran the MANOVA analysis (Table 2). Below-ground biomass and rhizome size (volume) were highly correlated ($r = 0.82$, $P = 0.0001$) and responded strongly to the experimental treatments; therefore, we assessed their combined effects with multivariate MANOVA. Florivory increased below-ground growth by almost 30% (Figure 2, Wilks’ $\lambda = 0.56$, $F_{2,24} = 9.91$, $P = 0.0007$). The three *I. hexagona* populations differed significantly in belowground growth (Figure 3, Wilks’ $\lambda = 0.64$, $F_{4,48} = 2.98$, $P = 0.028$). They also responded differently to salinity (Figure 4, Wilks’ $\lambda = 0.61$, $F_{4,48} = 3.31$, $P = 0.018$).

One year after the florivory experiment, 52% (± 6 SE) of treatment plants and 49% (± 2 SE) of control plants flowered. Browsed plants produced 16% more flowers than unbrowsed plants (average flowers per plant = 3.9 and 3.3, respectively, $F_{1,20} = 2.76$, $P = 0.112$). None of the main factors had a significant effect on flower numbers (model $F_{11,20}$

= 1.67, $P = 0.154$). Two interactions associated with flower production produced P -values less than 0.10: population \times salinity ($F_{2,20} = 3.39$, $P = 0.054$) and population \times salinity \times florivory ($F_{2,20} = 3.21$, $P = 0.062$).

DISCUSSION

Coastal wetlands are increasingly vulnerable to large-scale disturbances caused by natural and anthropogenic forces. The category III hurricanes that occurred in coastal Louisiana in 2005 exposed the fragility of wetland communities and awakened the public to their ecological importance. The increased salinity and flooding that occurred were severe and historic. Such storms are unlikely to be isolated events, and they indicate a growing trend of global warming and environmental change that will disproportionately affect coastal ecosystems. These changes will affect all members of the ecological community and the interactions between them. Research involving wetland ecosystems is crucial, not only to understand their underlying ecological processes, but to acquire the information necessary to predict future conditions and biological attributes of these remarkably dynamics habitats.

To our knowledge, this is the first record of widespread florivory in North American irises, which evolved with mammalian browsers and are well-defended by noxious chemical compounds (Craighead *et al.* 1963, Cornell University Poisonous Plants Database 2001). White-tailed deer selectively consumed approximately 80% of all of the flowers produced by *I. hexagona* growing in brackish habitats. Florivory is rare in freshwater *I. hexagona* populations, and in most years, florivory is positively correlated with iris population soil salinity levels (Geddes and Mopper 2006).

Why does salinity promote florivory? Little is known about the influence of salinity on interactions between freshwater plants and their herbivores. Previous studies have shown that salinity alters *I. hexagona* flowering phenology (Van Zandt and Mopper 2002), seed production (Van Zandt *et al.* 2003), seed germination (Van Zandt and Mopper

Table 1. Correlations among variables estimating *I. hexagona* performance in response to florivory, population, and salinity. Partial correlation coefficients (r) above and P -values below in parentheses.

	Above-ground biomass	Below-ground biomass	Rhizome number	Rhizome volume (cm ³)
Above-ground biomass	1	0.334 (0.14)	0.802 (0.0001)	0.664 (0.001)
Below-ground biomass		1	0.470 (0.031)	0.821 (0.0001)
Rhizome number			1	0.638 (0.002)

Table 2. Effects of florivory, population, and salinity on *I. hexagona* below-ground biomass and rhizome size. The data presented are from the univariate (A, B) and multivariate (C) reduced MANOVA output, which excludes the non-significant dependent variables (aboveground biomass, number of rhizomes) and main effects. Factors significant at $P < 0.05$ are shown in boldface.

A. Below-ground biomass (g)				
Source	DF	MS	F	P
Florivory	1	295204	17.99	0.0003
Population	2	112150	6.84	0.0043
Salinity	1	286	0.02	0.8960
Population*salinity	2	109972	6.70	0.0047
Error	25	16405		
B. Rhizome size (cm ³)				
Source	DF	MS	F	P
Florivory	1	29099	6.89	0.0145
Population	2	18693	4.43	0.0226
Salinity	1	19	0.00	0.9475
Population*salinity	2	10627	2.52	0.1009
Error	25	4221		
C. Combined response of below-ground biomass (g) and rhizome size (cm ³)				
Source	DF	Wilks' λ	F	P
Florivory	2,24	0.56	9.91	0.0007
Population	4,48	0.64	2.98	0.0280
Salinity	2,24	0.99	0.01	0.9888
Population*salinity	4,48	0.61	3.31	0.0179

2004), signaling hormones (Wang et al. 2001, Mopper et al. 2004), and interaction with insects herbivores (Schile and Mopper 2006). Irises are glycophytes and cannot excrete salt; it accumulates in plant tissues (Wang 2002) and may be attractive to deer. Salinity also eliminates glycophytic species preferred by deer in wetland communities. Our study *I. hexagona* populations inhabit a heterogeneous environment, where conditions shift from intermediate to brackish both spatially and temporally. Preferred deer forage is typically available (Linscombe et al. 1998), but dieback occurs when

salinity rises during tropical storms or drought (pers. comm., Edmond Mouton, Head Biologist State of Louisiana Department of Wildlife and Fisheries). As favored species become rare through overgrazing or other causes, pressures increase on less palatable vegetation (Johnson et al. 1995) such as iris flowers.

Consequences of Florivory

In non-clonal species, small amounts of florivory can reduce maternal fitness, fecundity, and seedling recruitment (Louda and Potvin 1995). Even though

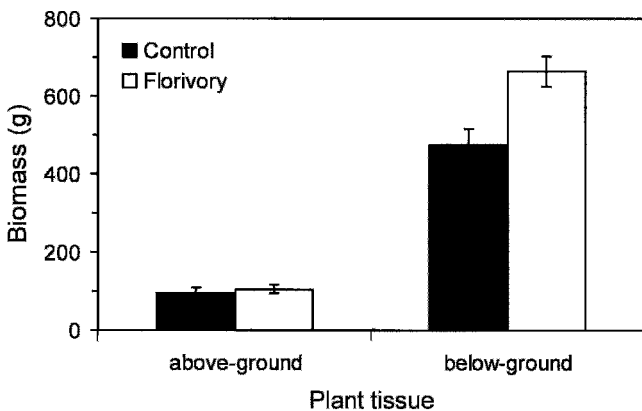


Figure 2. Effect of florivory on *I. hexagona* biomass (Wilks' lambda = 0.56, $F_{2,24} = 9.91$, $P = 0.0007$). Bars indicate standard errors.

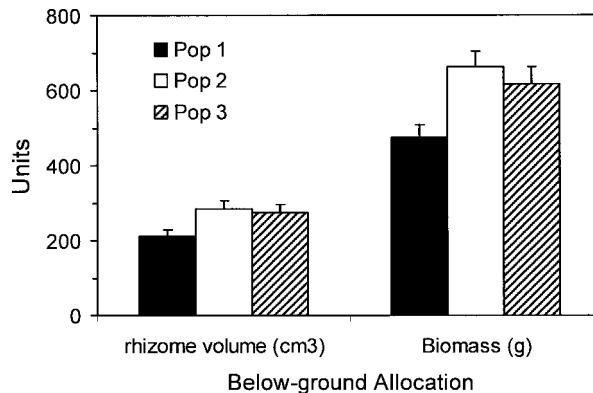


Figure 3. Rhizome size and below-ground biomass produced by three *I. hexagona* populations (Wilks' lambda = 0.64, $F_{4,48} = 2.98$, $P = 0.028$). Bars indicate standard errors.

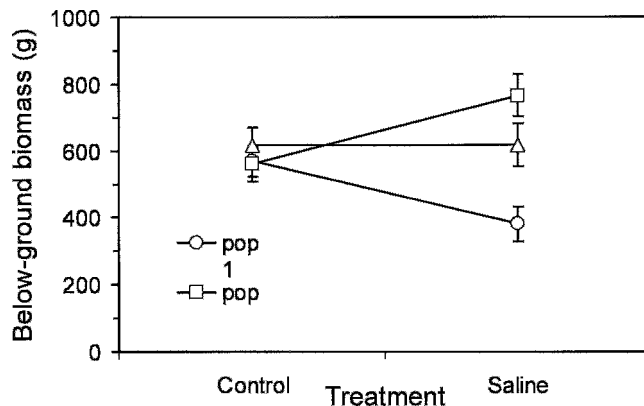


Figure 4. Different responses of three *I. hexagona* populations to salinity (Wilks' lambda = 0.61, $F_{4,48} = 3.31$, $P = 0.018$). The low salinity (control) treatment = $0.2 \pm 0.4 \mu\text{g g}^{-1}$ and high salinity = $4.6 \pm 1.2 \mu\text{g g}^{-1}$. Bars indicate standard errors.

strictly sexual species can compensate for lost floral structures, to do so requires either multiple inflorescences (Lowenberg 1997) or the ability to regenerate reproductive structures such that a single bout of florivory does not eradicate all reproduction in the year it occurs (Paige and Whitham 1987). Clonal reproduction is an effective mechanism to tolerate and perhaps benefit from lost sexual reproduction (Pan and Price 2001). For example, experimental removal of inflorescence buds significantly increased tuber number and below-ground biomass in the clonal perennial, *Helianthus tuberosus* (Westley 1993). On average, *I. hexagona* plants are composed of 12% leaves, 20% sexual structures, 31% roots, and 37% clonal rhizomes (Figure 5). Since below- and above-ground structures compete for resources (Lytle and Hull 1980, Casper and Jackson 1997), the balance between them may shift when herbivory or florivory occurs.

By stimulating clonal growth, deer may benefit *I. hexagona* plants because below-ground allocation can enhance populations (Kingsolver 1986) and ecosystems (Eriksson 2000, Turner *et al.* 2004). For example, the resources diverted to below-ground structures when flowers are removed could ameliorate environmental disturbance by stabilizing plants (Combroux *et al.* 2002). Bare *I. hexagona* rhizomes that have been exposed to light by fire or flooding rapidly become photosynthetic and produce new foliage (S. Mopper, pers. obs.). Clonal structures can have non-reproductive functions and play critical roles in re-establishing plants after environmental stress or disturbance.

Although florivory immediately reduces fertility, it may improve future opportunities for recombination because the long-lived genets will experience

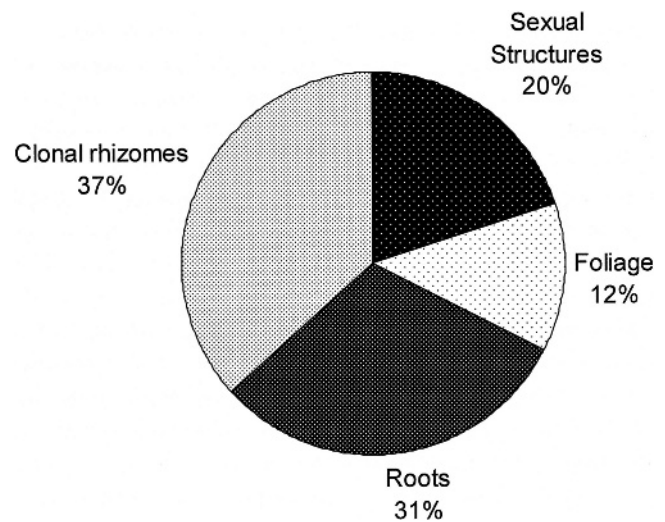


Figure 5. Distribution of plant resources allocated to sexual and vegetative structures, based on average mass. Sexual structures include flowers, flower stems, seed capsules, and seeds.

random mutations, eventually separate from maternal plants, and produce new individuals with the potential to reproduce sexually (Burke *et al.* 2000). The population-by-salinity interactions we observed in this study and in a separate experiment (Van Zandt *et al.* 2003) suggest that *I. hexagona* may be differentially adapted to environmental variables such as salinity. Recent analysis of microsatellite markers indicates substantial heterozygosity within and among *I. hexagona* populations (Z. He, A. Meerow and S. Mopper, unpublished data). Such high levels of genetic diversity indicate that florivory is not consistently high and may be governed by temporal variation in abiotic conditions and fluctuations in deer populations.

Interactions between Salinity and Florivory

The influence of florivory and salinity on *I. hexagona* is complex because of its ability to allocate resources to clonal and sexual reproduction. Although salinity had little direct effect on iris performance in our 12-month florivory experiment, exposure for 20 months to the same level of salinity ($\sim 4 \mu\text{g g}^{-1}$) markedly reduced growth, and low levels of salt ($\sim 2 \mu\text{g g}^{-1}$) stimulated seed production significantly (Van Zandt *et al.* 2003). Fluctuation between salinity stress, which promotes fertility, and florivory, which enhances clonal growth, may have facilitated the adaptation and persistence of *I. hexagona* during Marsh Island's gradual isolation and shift from freshwater to brackish conditions.

The distinct population responses to salinity and florivory also suggest different reproductive strategies indicative of adaptive variation (Mousseau et al. 2000). The *I. hexagona* population producing the greatest number of flowers and largest biomass in our experiment was the most vigorous out of ten populations studied in a previous independent experiment (Van Zandt et al. 2003), suggesting strong genetic control over these traits. The large assemblage of isolated *I. hexagona* populations that occasionally exchange genes and resist disturbance through clonal growth, may represent a stable metapopulation that can adapt and persist in changing environments (Wright 1978, Wade and Griesemer 1998). Ecologists have long recognized that explosive growth in deer densities can affect plant communities through overgrazing, but there is much to be learned about the ecological forces underlying interactions between deer and plant populations (Russell et al. 2001). Our study demonstrates that abiotic conditions such as salinity can have profound and complex effects on vertebrate herbivores and the plants they consume.

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