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ABSTRACT

Populations of the floating macrophyte, *Salvinia minima* Baker, were assessed over a 39-month period at four sites in southern Florida in order to elucidate the abiotic and biotic factors that influenced their density. These factors included the abundance of other plant species, changes in water depth, water quality, and herbivory by insects. Abiotic factors like temperature, pH, DO, and conductivity varied among sites and, more importantly, over time. The same was true for *S. minima* biomass, coverage, and condition. Principal component analysis identified four components which together explained 64% of the variability in *S. minima* biomass. The first component correlated strongly with herbivory from *Cyrtobagous salviniae* Calder and Sands and *Synclita obliteralis* (Walker) as well as the abundance of the duckweed *Spirodela polyrrhiza* (L.) Schleid. Temperature effects were strongly represented in the second principal component. A stepwise regression model that best predicted *S. minima* biomass incorporated conductivity, insect herbivory, and interspecific plant abundance. Broader dry vs. wet season influences were apparent and linked to temperature, water depth, and conductivity that covaried with *S. minima* biomass. Sites where water depth changed the most had the least *S. minima*. Insect herbivory did not increase under more stagnant conditions when plant populations were less mobile. Overall, *S. minima* populations cycled in southern Florida in response to a shifting array of abiotic and biotic factors. The relative importance of these factors was less clear although the influences of herbivory, temperature, and the presence of other plants were significant.

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1. Introduction

Herbivory, competition, water quality, hydrology, and their interactions contribute to the structuring of aquatic plant communities (Webb et al., 2006; Harpole and Suding, 2007; Grime, 1973; Tipping et al., 2009). Floating macrophytes in particular experience dynamic forces that are unique among plants, namely a movable substrate whose habitat location, nutrient profile, depth, current, and competing vegetation can change rapidly and unpredictably. These forces likely interact simultaneously along a continuum of temporal and spatial levels and their relative contribution is probably context-specific. For example, in a highly disturbed site where water levels and currents are more dynamic, factors like herbivory and nutrients may interact differently than in stagnant water.

This study assessed in situ stands of common salvinia, *Salvinia minima* Baker, at specific sites in southern Florida with the aim of elucidating the biotic and abiotic factors that influenced its population dynamics. We hypothesized that top-down effects like herbivory by specialist herbivores such as *Cyrtobagous salviniae* Calder and Sands (Coleoptera: Curculionidae), along with generalists like *Samea multiplicalus* (Guenée) (Lepidoptera: Pyralidae) and *Synclita obliteratis* (Walker) (Lepidoptera: Pyralidae), would be a primary factor in regulating *S. minima*.

2. Materials and methods

2.1. The study plant

Salvinia minima is an exotic floating macrophyte common to freshwater drainages in Florida. Native to Central and South America, this species was probably introduced into the U.S. through the aquarium trade (Stoltze, 1983; Mickel and Beitel, 1988). It was first reported in Florida in the St. Johns River in 1928 and currently inhabits a wide range of fresh water natural and man-made habitats including sloughs, cypress swamps, lakes, and canals under a continuum of shading conditions (Small, 1931). Jacono et al. (2001) documented the spread of this species throughout Florida and along the Gulf coast. Although this species is considered noxious in several states, its pest status in Florida is relatively minor compared

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Table 1
Locations and descriptions of experimental sites in southern Florida with persistent populations of *S. minima*.

Name	GPS	Habitat	Associated aquatic plants	Area (km^{-2})
Loxahatchee Visitors Center	26° 29′58.10″ N 80°12′45.08″W	Pond	*Spirodela polyrrhiza* (L.) Schleid.	0.002
Corkscrew Swamp Sanctuary	26°22′33.09″N 81°36′32.05″W	Slough	*Limnobium spongia* (Bosc.) Steud. *Azolla caroliniana* Will., *Thalia geniculata* L., *Polygonum punctatum* Ell.	20.0
Fisheating Creek	26°55′51.44″N 81°18′52.78″W	Oxbow	*Eichhornia crassipes* (Mart.) Solms.	0.05
Loxachatchee Swamp	26°29′55.64″N 80°12′51.36″W	Swamp Forest	*Pistia stratiotes* L., *A. caroliniana*	1.5

with states like Louisiana where the plant is considered a significant problem. One difference between these states is the presence of the specialist herbivore *C. salviniae* in Florida. This weevil was first detected in 1962, although it may have been present earlier, and was probably introduced along with the plant (Kissinger, 1966).

2.2. Sampling method

Four field sites were monitored monthly from April 2002 through July 2005: (1) Fisheating Creek (FEC), (2) the Audubon Corkscrew Swamp Sanctuary (Cork), and two sites in the Arthur R. Marshall Loxahatchee National Wildlife Refuge: (3) Visitors Center (LoxVC) and (4) Loxahatchee Swamp (LoxSW). The habitats ranged from natural sloughs to oxbow lakes that contained persistent populations of *S. minima* (Table 1).

Sites were visited once a month and three samples from each of four permanent transects were collected within each site. These transects were established using landmarks and GPS. Sampling of plant cover and biomass was conducted using 0.1 m^2 floating pvc frames placed haphazardly within transects. Plant coverage by all species within the sample frames was estimated visually to the nearest 10% by two observers. Brown coloration of *S. minima* mats has been associated with insect-damaged and weakened plants as with *S. molesta* (Room et al., 1981), so a visual estimate was also made of the percentage of the *S. minima* mat that appeared green vs. brown, estimated to the nearest 25% within the ranges of 0, 1–24, 25–49, 50–74, 75–99, and 100%. All the *S. mimima* was then collected from the samples and first processed through a Berlese funnel for 72 h to force out herbivorous insects into collection jars stocked with a few live *S. minima* plants. The number and weights of adult *C. salviniae* were recorded and a subset of adults was sacrificed to check for the presence of microsporidia. No biomass or pathogen measurements were taken from other herbivores on *S. minima* or other plant species. Plant samples were dried to a constant weight to obtain dry weight biomass. Whole plants were used to determine the carbon and nitrogen concentration in live tissues with a CHN analyzer. The leaf size of *S. minima* was estimated by haphazardly selecting 10 ramets per transect and measuring the length of the long axis of two leaves at the second internode proximal from the apical bud of each ramet. Water depth, pH, water temperature, DO, and conductivity were recorded in sample squares using a variety of hand-held meters. Air temperature was measured at the first transect of each site.

Principal components analysis was used to characterize the variation in the sample data. Variables that appeared to influence *S. minima* biomass were further subjected to forward stepwise regression. The influence of several variables was also directly examined using repeated measures ANOVA. Variable means were separated post hoc using Tukey's HSD or *t*-tests. All statistical analyses were conducted using SAS v9 (SAS, 2000).

3. Results

There were substantial differences in *S. minima* biomass, % coverage, and % green among sites and over time (Table 2). The influence of date (time) was the most important while the influence of transects was insignificant. There was also a significant site x date interaction for all the variables (Table 2). Abiotic factors like water temperature, water quality, and the change in water depth between samples also varied among sites (Table 3). Nitrogen levels, as measured in *S. minima* tissue, did not differ among sites, ranging from 2.25% to 2.32% of DW. The smallest weevils were found at Cork and LoxSW (0.67 ± 0.01 mg and 0.70 ± 0.02 mg, respectively) and the largest at FEC and LoxVC (0.76 ± 0.02 mg for both sites).

Combining all variables from all field sites yielded four principal components with each accounting for at least 8% of the variation, while cumulatively accounting for 64% of the total variability (Table 4). The first principal component explained 26% of the total variance and was interpreted as complex of factors related to insect herbivory and the abundance of small floating plants found in the same niche as *S. minima*. The second principal component explained 14% of the variation and reflected the influence of

Table 2
Results of ANOVA for biotic and abiotic variables with site, transect, and date as main factors. Site x date was the only significant interaction. The effect of transect was not significant except for depth (df = 3, TSS = 4%, P = 0.001).

Variables	Site			Date			Site × Date		
	df	TSS (%)	*P*	df	TSS (%)	*P*	df	TSS (%)	*P*
Total biomass (g DW m^{-2})	3	5	0.001	30	24	0.001	90	39	0.001
Percent cover (m^{-2})	3	3	0.001	30	29	0.001	90	38	0.001
Percent green (m^{-2})	3	15	0.001	30	26	0.001	90	31	0.001
Depth (cm)	3	18	0.001	30	36	0.001	90	27	0.001
Air temperature (°C)	3	9	0.001	30	81	0.001	90	11	0.001
DO (mg L^{-1})	3	10	0.001	27	55	0.001	61	34	0.001
Conductivity (mS cm^{-1})	3	53	0.001	28	18	0.001	64	28	0.001
Water temperature (°C)	3	1	0.01	30	95	0.001	90	4	0.001
pH	3	3	0.001	27	77	0.001	61	19	0.001

Presented are the degrees of freedom (df), the rounded percentage of variance explained by a factor (TSS = (100 × factor SS)/total SS), and the level of significance (*P*) for 31 sample dates common to all sites. Air temperature was recorded only at the first transect at each site.

Table 3
Means (±SE) of environmental and biological variables for sample sites during April 2002 through July 2005. The number of observations taken is listed in parentheses after each mean.

Variable	Sample site[a]			
	Cork	FEC	LoxSW	LoxVC
Water temperature (°C)	22.2 ± 0.4 a (116)	20.9 ± 0.4 d (124)	21.8 ± 0.4 b (100)	21.4 ± 0.4 c (132)
DO ($mg\,L^{-1}$)	2.1 ± 0.1 a (116)	0.9 ± 0.1 c (120)	1.9 ± 0.1 a (100)	1.6 ± 0.1 b (132)
pH	6.4 ± 0.1 c (112)	6.5 ± 0.1 bc (114)	6.5 ± 0.05 b (90)	6.7 ± 0.07 a (120)
Conductivity ($mS\,cm^{-1}$)	0.3 ± 0.005 c (116)	0.19 ± 0.005 d (124)	0.37 ± 0.01 b (100)	0.4 ± 0.008 a (132)
Depth (cm)	85.6 ± 3.0 a (116)	65.1 ± 4.1 c (124)	37.3 ± 2.2 d (100)	76.6 ± 2.1 b (132)
Depth change (cm)[b]	21.3 ± 2.3 b	35.7 ± 3.3 a	14.4 ± 1.5 c	15.4 ± 1.3 c
S. minima biomass ($g\,DW\,m^{-2}$)	20.9 ± 2.2 b (116)	23.1 ± 2.2 b (124)	35.5 ± 3.7 a (100)	37.3 ± 3.6 a (132)

[a] Means across rows followed by different letters are significantly different at $P < 0.05$ using Tukey's HSD (SAS, 2000).
[b] Depth change is calculated as the mean change in depth between consecutive samples.

temperature, while the third component (11% variation) reflected a less equivocal complex of wet and dry seasonality characteristics, primarily conductivity and water depth, along with coverage by larger floating plants and larger *S. minima* plants. The fourth principal component was not listed in Table 4 (only 8% variation explained) but was interpreted as disturbance as measured by the mean change in water depth between sample dates.

Stepwise regression identified conductivity as the most important of several predictive variables for *S. minima* biomass, which also included the insect herbivores *C. salviniae* and *Synclita obliteralis* and the abundance of the aquatic plants *Spirodela polyrrhiza* and *Limnobium spongia* (Table 5).

4. Discussion

Herbivory and interspecific plant abundance appeared to play an important role in explaining the variation in *S. minima* populations. Therefore, our hypothesis on the importance of herbivory was supported. At the same time, the role of other plant species that occupy the same niche as *S. minima* is yet unclear. If competition is occurring, it can have profound effects on plants in the presence of herbivory, leading to disproportionate reductions in biomass and other measures of fitness (Center et al., 2005). The influence of these and other biotic factors may depend on the characteristics of the physical environment (Brooker and Callaghan, 1998). In this study, the range of these physical forces was reflected in the seasonality of southern Florida primarily through temperature, and secondarily through depth and conductivity. This included water depth which was lower during the dry season (63.2 ± 2.04 cm [dry] vs. 72.4 ± 2.7 cm [wet]; $t_{474} = 2.72$, $P < 0.006$) to the point where some areas became temporarily stagnant. Mean (±SE) conductivity was concomitantly higher during this time (0.32 ± 0.01 $mS\,cm^{-1}$ [dry] vs. 0.29 ± 0.01 $mS\,cm^{-1}$ [wet]; $t_{426} = 2.4$, $P < 0.01$).

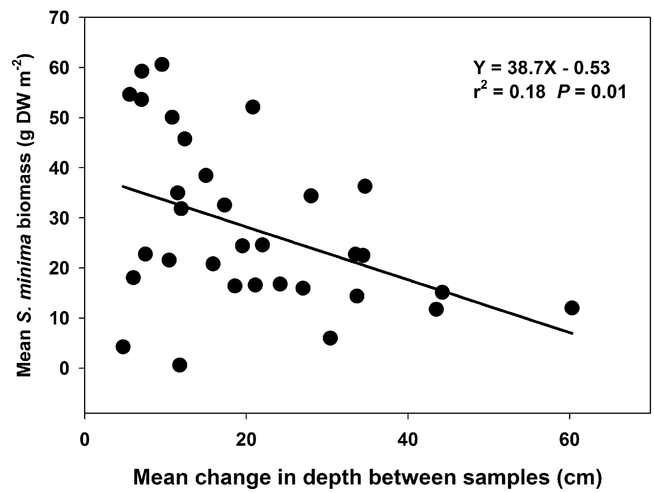

Fig. 1. Relationship between the mean percent change in water depth between samples and *S. minima* biomass.

Changes in depth, as measured between sampling periods not seasons, was another physical force with important consequences for small floating plants like *S. minima*, as evidenced by reduced biomass with greater changes in depth (Fig. 1). The hydrologically

Table 4
Correlations of abiotic and biotic variables[a] in four sites in southern Florida with the first three components of a principal component analysis (56% explained variance).

Principal component[b] (% of variance explained)	PC1 (27%)	PC2 (17%)	PC3 (12%)
Air temperature	−0.09	**0.79**	0.27
Dissolved oxygen	−0.19	−**0.75**	0.07
Salinity	0.17	−0.16	−**0.65**
Water temperature	−0.15	**0.85**	0.17
Depth	0.08	0.05	**0.72**
S. minima coverage	−**0.69**	0.02	−0.18
S. polyrrhiza coverage	**0.87**	−0.03	−0.15
L. spongia coverage	−0.09	0.18	**0.72**
No. *C. salviniae* per g of *S. minima*	**0.54**	0.09	0.20
No. *S. obliteratis* per g of *S. minima*	**0.82**	0.01	0.03
Percentage of *S. minima* buds damaged	**0.51**	0.16	0.11
Size of *S. minima* leaves	0.26	−0.03	**0.59**

A fourth principal component explained another 8% of the variation and was interpreted as disturbance caused by the change in water depth between sample dates. Coefficients greater than ±0.4 are considered informative and shown in bold. Variables with coefficients less than ±0.4 in any of these three principal components are omitted.
[a] Omitted variables: pH, flow rate, change in depth between samples, coverage of *E. crassipes*, *P. stratiotes*, and *A. caroliniana*, percentage of the *S. minima* mat that was green, individual *C. salviniae* biomass, number of *C. salviniae* infected with pathogens, number of *S. multiplicalis*, percent parasitism of *S. multiplicalis* and *S. obliteralis*, and CN ratio of *S. minima* tissue.
[b] The first component is interpreted as a construct of factors related to insect herbivory and the abundance of small floating plants that might compete with *S. minima* for space, the second to temperature, and the third to a combination of seasonal influences on water quality as well as the abundance of larger plant species.

Table 5
Stepwise forward regression of *S. minima* biomass across all sites with independent abiotic and biotic variables.

Dependent	Step	Independent variable	r^2	p	Slope
S. minima biomass	1	Conductivity	0.13	0.0001	115.17
	2	No. *C. salviniae*	0.22	0.0001	0.31
	3	Coverage by *S. polyrrhiza*	0.29	0.0001	−0.50
	4	No. *O. obliteralis*	0.35	0.0001	0.09
	5	Coverage by *L. spongia*	0.39	0.0001	−0.56
	6	Air temperature	0.41	0.002	−1.29
	7	Water depth	0.42	0.005	0.13

List of independent variables entered to select from: air temperature, DO, conductivity, water temperature, depth, change in depth between samples, coverage by *S. minima*, *S. polyrrhiza*, and *L. spongia*, number of *C. salviniae* and *S. obliteralis* per g of *S. minima*, percent of damaged *S. minima* buds, and size of *S. minima* leaves. Presented are the explained cumulative variance (r^2), the level of significance of each added variable, and the slope.

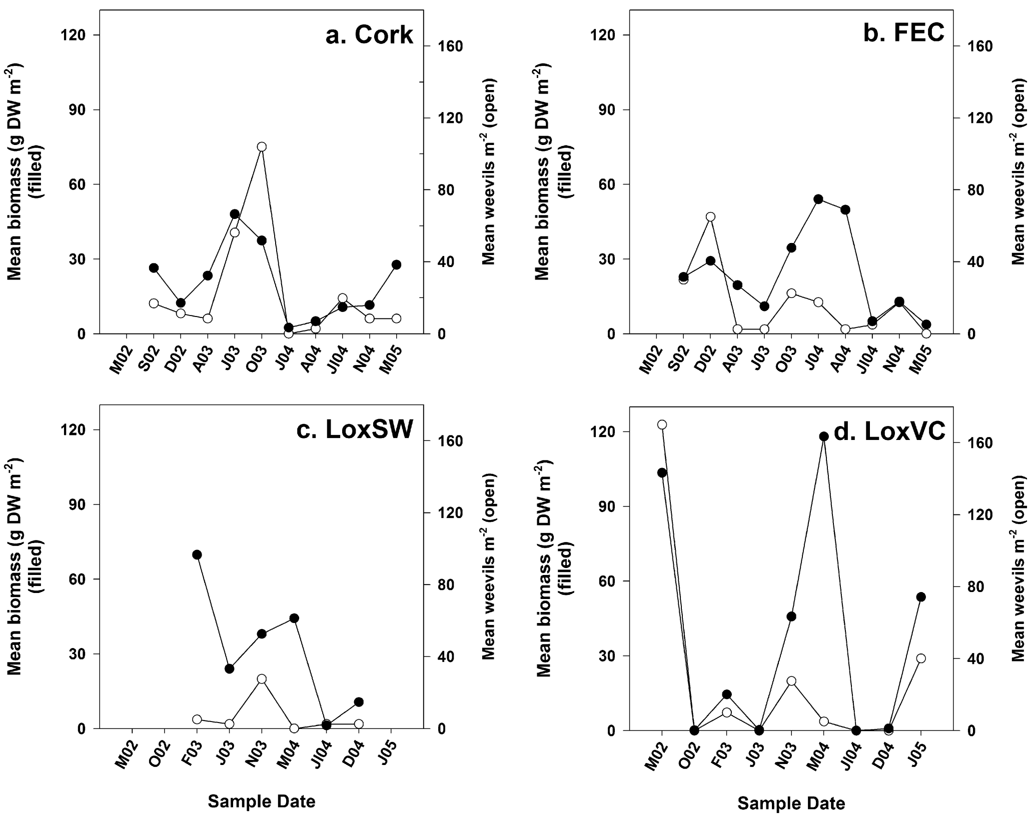

Fig. 2. Plots of *S. minima* biomass (filled symbols) and numbers of *C. salviniae* (open symbols) recorded at: (a) Corkscrew Swamp Sanctuary, (b) Fisheating Creek, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge sites (c) Swamp, and (d) Visitor's Center. Some dates have been omitted to improve legibility.

more variable sites like Cork and FEC had less *S. minima* (Table 3). Seasonality was linked to changes in depth with a 28.2 ± 3.2% mean monthly change during the dry season compared with a 67.3 ± 9.3% change during the wet season (t_{462} = 4.1, P < 0.0001). Although more stagnant conditions promoted greater biomass densities, these relatively immobile plant populations did not experience higher levels of herbivory, neither from *C. salviniae* (P = 0.48) whose adults are more likely to disperse locally by walking on mats rather than flying, nor from defoliators whose adults readily fly (P = 0.77). Instead, weevil numbers appeared to roughly track *S. minima* biomass at all sites regardless of the disturbance caused by changes in depth (Fig. 2).

Although we did find *Nosema* sp. pathogens in *C. salviniae* in two consecutive sample dates (August–September, 2003) at one site (LoxVC), the amount of infection was considered to be very light (G. White, personal communication). This is not the first record of pathogen infection for this species: White et al. (2007) found a parasitic alga, *Helicosporidium* sp., in a shipment of *C. salviniae* from South Africa. Therefore, it appears unlikely that pathogens may periodically weaken populations of *C. salviniae* and thereby indirectly influence *S. minima* populations.

This study documented population cycles of *S. minima* in southern Florida in response to a shifting array of abiotic and biotic factors. The hierarchy of their importance was less clear although the importance of herbivory as a biotic factor was apparent. *Salvinia minima* populations, with their ability to grow quickly, move passively, and grow in shaded conditions were found to be fairly resilient across time and space.

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