

Competition between *Salvinia minima* and *Spirodela polyrhiza* mediated by nutrient levels and herbivory

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ABSTRACT

We investigated the effects of initial biomass, nutrients, herbivory, and competition with *Spirodela polyrhiza* (L.) Schleid on *Salvinia minima* Baker biomass and density. *S. minima* populations were subjected to two levels of herbivory (control vs. two adults per plant) from the weevil *Cyrtobagous salviniae* Calder and Sands and eight levels of competition from *S. polyrhiza*, while growing in high (5 mg N l⁻¹) or low (0.5 mg N l⁻¹) nutrient conditions. Herbivory was the most important factor in *S. minima* biomass production while competition or fertility had no measurable impact. In contrast, *S. polyrhiza* biomass was mediated primarily by nutrients, not competition. There was no herbivory treatment for this plant. *S. polyrhiza* was superior to *S. minima* at converting nutrients to biomass but this did not give it a competitive advantage since *S. minima* biomass was unchanged when herbivory was absent. *S. minima* can generally overtop *S. polyrhiza* which, in turn, can form multiple layers within its mat. These characteristics may act to lessen competition between these species, thereby permitting their habitat sharing.

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1. Introduction

Floating macrophytes, like all plants, compete for space, light, and nutrients along a gradient of biotic and abiotic factors. There are no comparable terrestrial equivalents to these passively mobile plants which obtain nutrients directly from the water. The dynamic nature of their growing medium complicates attempts to predict their assemblages and densities under natural conditions. McLay (1974) and Jacobs (1947) listed several abiotic and biotic factors that varied both spatially and temporally and influenced the distribution and densities of floating macrophytes including pH, currents, wind, aquatic animals, and water depth.

Gopal and Goel (1993) opined that competition in aquatic environments is expected to occur most between species of similar growth forms occupying identical positions in the water column. Most competition studies involving vegetatively reproducing, free-floating macrophytes have focused on their intrinsic or relative growth rates in pure and mixed cultures in order to rank their competitive abilities (Clatworthy and Harper, 1962; Reddy and Debusk, 1985). These types of studies have led to predictions that species with higher growth rates will dominate the early stages of

succession (Goldberg, 1990). However, it is likely that many additional factors will influence these competitive outcomes including phylogeny (Darwin, 1859; Webb et al., 2006; Maherali and Klironomos, 2007), intraspecific competition (Weiner, 1990; Harpole and Suding, 2007), resource availability (Grime, 1973), herbivory (Crawley, 1989), and their interactions (Bertness and Callaway, 1994).

Nutrient availability influences plant community structure in natural aquatic environments (Tilman, 1984). Van et al. (1999) found that *Hydrilla verticillata* was more competitive than *Vallisneria americana* at high fertility conditions but the reverse was true under nutrient limiting conditions. However, superiority in terms of growth rates or the ability to compete for nutrients can be offset by morphology. For example, McIlraith et al. (1989) described how *Lemna trisulca*, a better competitor for nutrients than the associated *Lemna minor*, was nonetheless excluded from certain environments after being overtopped by *L. minor*. Clatworthy and Harper (1962) found that success in mixed species was based on attaining higher relative positions which enabled them to shade competitors.

Herbivory is yet another factor that can influence competitive interactions by differentially suppressing species (Crawley, 1989). Fowler and Antonovics (1981) suggested that although interference between plants occurs primarily between neighboring individuals, the action of predators or pathogens may extend the

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radius of the effect of an individual. Competitive shifts have been documented along a herbivory continuum between plants for both submerged (Gross et al., 2001; Van et al., 1998) and floating species (Center et al., 2005).

The nutritional status of the plant (as influenced by the environment) can further complicate outcomes. Populations of insect herbivores may increase in response to more nutritious plants, a common result of growing in more eutrophic conditions (Room, 1990; Heard and Winterton, 2000). Although these plants may experience increased herbivory, they may compensate for damage with vigorous growth (Coley, 1983). Contrary outcomes are also possible: higher fertility plants can also suffer disproportionate damage by herbivores whose own fecundity is enhanced by the nutrient status of their host (Oksanen et al., 1981). However, Center et al. (2005) found that although the nutritional status of *Eichhornia crassipes* influenced individual herbivore performances, the overall suppressive herbivore effect on plants was not influenced by nutrition.

Salvinia minima Baker and *Spirodela polyrhiza* (L.) Schleid are floating macrophytes commonly found growing together in freshwater habitats in Florida. Both are highly competitive species that reproduce vegetatively. *S. minima* is an exotic species in the U.S. whose native range includes Mexico south to Argentina (Stoltze, 1983; Mickel and Beitel, 1988). It was first described in the U.S. in 1928 from the St. Johns River in Florida (Small, 1931). Jacono et al. (2001) summarized the first detections and spread of this species in the U.S. *S. polyrhiza* has a cosmopolitan distribution throughout most temperate and tropical regions (Daubs, 1965). In North America its range extends from southern Canada southward throughout the United States (Jacobs, 1947).

Although exotic species rarely have specialized herbivores in their adventive ranges, *S. minima* in Florida is an exception because of the presence of *Cyrtobagous salviniae* Calder and Sands (Coleoptera: Curculionidae) (Kissinger, 1966). Jacono et al. (2001) stated that this weevil species, initially misidentified as *Cyrtobagous singularis*, was first collected sometime before 1960. It is likely that this small (1–3 mm length), inconspicuous insect was introduced at some point with the plant, perhaps through the aquarium trade. Adults feed on leaves and buds while the larvae generally tunnel through the rhizomes. This plant is also attacked in the field by generalist herbivores like *Samea multiplicalus* (Guenée) (Lepidoptera: Pyralidae) and *Synclita oblitalis* (Walker) (Lepidoptera: Pyralidae) (Tipping and Center, 2005). The herbivore guild on *S. polyrhiza* is less well known although the plant is sometimes attacked by *Tanyssphyrus lemnae* Paykull (Coleoptera: Curculionidae), *S. oblitalis*, *Lemnaphila scotlandae* Cresson (Diptera: Ephydriidae), and gastropods but their impacts are unknown (Scotland, 1940; Tanner, 1943; Sahai and Roy, 1977; McIlraith et al., 1989).

Our objective was to examine the influence of initial biomass, nutrients, and herbivory on *S. minima* on the competitive interactions between *S. minima* (hereafter salvinia) and *S. polyrhiza* (hereafter spirodela). We hypothesized that (1) herbivory on *S. minima* would negate any initial biomass or morphological advantage thereby promoting *S. polyrhiza* and (2) both species would respond equally to increased fertility.

2. Materials and methods

Mixtures of salvinia and spirodela were grown outside in concrete tanks (0.8 m wide × 2.2 m long × 0.65 m deep) at the USDA-ARS Invasive Plant Research Laboratory in Ft. Lauderdale, FL (26°12'N, 80°53'W). Original colonies of salvinia and spirodela used in this experiment were obtained from local water bodies. Individual ramets are called plants in this study. Factorial

combinations of salvinia (mean ± S.E. dry weight = 2.7 ± 0.06 mg plant⁻¹) plants and their equivalent biomass of spirodela (mean ± S.E. dry weight = 0.07 ± 0.003 mg plant⁻¹) were added to tanks filled to a volume of 972 l. Plant ratios were based on the number of salvinia plants and consisted of 0:3, 0:9, 3:0, 3:3, 3:9, 9:0, 9:3, and 9:9 salvinia plants:spirodela biomass equivalents. For example, the 3:3 ratio consisted of 3 salvinia plants and the equivalent biomass of spirodela or 116 spirodela plants. Every plant was examined under a dissecting microscope prior to deployment in order to ensure they were not infested by invertebrates.

Each biomass combination was grown in 0.1 m² floating frames and nested factorially within the nutrient and herbivory treatments in a randomized complete block design. Herbivory was evaluated only with salvinia by using a control treatment with no *C. salviniae* adults and a release treatment where two adults (1:1 ♀:♂) were released per salvinia plant. There was no comparable herbivore available for spirodela. Screens which prevented the adults from moving among frames intercepted about 50% of available natural light. Mean (±S.E.) solar radiation was 955 ± 42.5 μmol m⁻² s⁻¹ (n = 512) at 1200 and 1300 EST US during the course of this study. Nutrients were added to achieve initial levels of 0.5 mg N l⁻¹ (low fertility) or 5 mg N l⁻¹ (high fertility) using soluble fertilizer (20% N, 20% P₂O₅, 20% K₂O, 0.5% Mg, 0.02% B, 0.05% Cu, 0.1% Fe, 0.05% Mn, 0.0005% Mo, 0.05% Zn) applied directly to the water when the plants were first placed (water pH = 8.3) and another application 14 days later. Treatments were replicated four times and the experiment was started on August 16, 2001 and ended October 18, 2001 after which plants were harvested and dried to determine dry weight biomass.

Data were analyzed using multivariate analysis of variance (MANOVA) to elucidate the effects of herbivory, nutrients, competition, and their interactions on the final biomass of salvinia and spirodela (SAS Institute, 1999). Roy's greatest root was used to test for significant differences between groups (Roy, 1953). SAS defines this eigenvalue as λ₁ which is developed from generalizing a univariate ANOVA from the analysis of a single dependent variable to the analysis of the linear combinations of several dependent variables that maximizes *F* (Kuhfeld, 1986). Canonical analysis (CANONICAL option of the MANOVA statement) (SAS Institute, 1999) was used to explain the relationship between the sets of variables used in this study. Standardized canonical coefficients were calculated from this analysis to illustrate the relative significant contribution of the response variables to the variation between groups (Scheiner, 1993). Values were transformed using square root transformation when variances were heterogeneous.

3. Results

Biomass production by both species was influenced by all the main factors and two interactions, namely (1) nutrients with initial spirodela biomass and (2) weevil treatment with initial salvinia biomass (Table 1). These interactions were primary and appeared to be species-specific. For example, fertility influenced spirodela but not salvinia, while herbivory influenced salvinia but had no secondary effect on spirodela (Fig. 1). The relative magnitudes of the canonical coefficients offer some insights (Table 2). For example, fertility disproportionately affected spirodela (Table 2). The main effect of the weevil treatment (CS) was expressed by changes in salvinia biomass (Table 2). Finally, the initial biomass of each species (SM or SP) best explained the differences in their final biomass (Table 2). These results lead us to reject both hypotheses, namely that herbivory on salvinia would ultimately benefit spirodela, and that both species would respond equally to fertility.

Table 1

Values of Roy's greatest root derived from multivariate analysis of the effects of fertility (N), herbivory (CS), initial plant number (SM), and equivalent initial plant number (SP) on the final biomass of *Salvinia minima* and *Spirodella polyrhiza*.

Source	Value	F	Num DF	Den DF	P
Fertility (N)	1.0878	51.67	1	96	<0.0001
<i>C. salvinia</i> (CS)	0.2245	10.67	1	96	<0.0001
Initial <i>S. minima</i> (SM)	0.2287	10.98	2	96	<0.0001
Initial <i>S. polyrhiza</i> (SP)	0.7025	33.72	2	96	<0.0001
N*CS	0.0155	0.74	2	96	0.4794
N*SM	0.0257	1.23	2	96	0.2955
N*SP	0.6012	28.86	2	96	<0.0001
N*CS*SM	0.0023	0.11	2	96	0.8933
N*CS*SP	0.0112	0.54	2	96	0.5847
N*SM*SP	0.0108	0.35	3	96	0.7909
N*CS*SM*SP	0.0169	0.54	3	96	0.6547
CS*SM	0.1814	8.71	2	96	0.0003
CS*SP	0.0115	0.55	2	96	0.5770
CS*SM*SP	0.0038	0.12	3	96	0.9461
SM*SP	0.0017	0.06	3	96	0.9825

4. Discussion

According to Clatworthy and Harper (1962), salvinia should outcompete spirodela morphologically by simply overtopping and

Table 2

Standardized canonical coefficients derived from multivariate analysis of variance.

	Final <i>S. minima</i> biomass	Final <i>S. polyrhiza</i> biomass
Fertility (N)	0.1953	1.6786
<i>C. salvinia</i> (CS)	1.1044	0.5468
Initial <i>S. minima</i> (SM)	1.0736	0.7062
Initial <i>S. polyrhiza</i> (SP)	0.1423	1.6816
N*SP	0.0209	1.6744
CS*SM	1.1260	0.3508

shading it. Dickinson and Miller (1998) found this to be true in a sheltered swamp. In our study, spirodela was often found under the fronds of salvinia, especially when the fronds did not lay directly on the water's surface and, in some cases, actually lifted the fronds off the water. However, spirodela may have minimized the impact of this overtopping by forming multilayered mats, a condition which is common in the field (Tipping, unpublished data). Multiple layers permit greater plant densities and their photosynthetic functionality may be facilitated by water movement, whereby waves may expose (albeit temporally) a greater percentage of the spirodela population to light resources than would otherwise be exposed in a relatively static medium like soil.

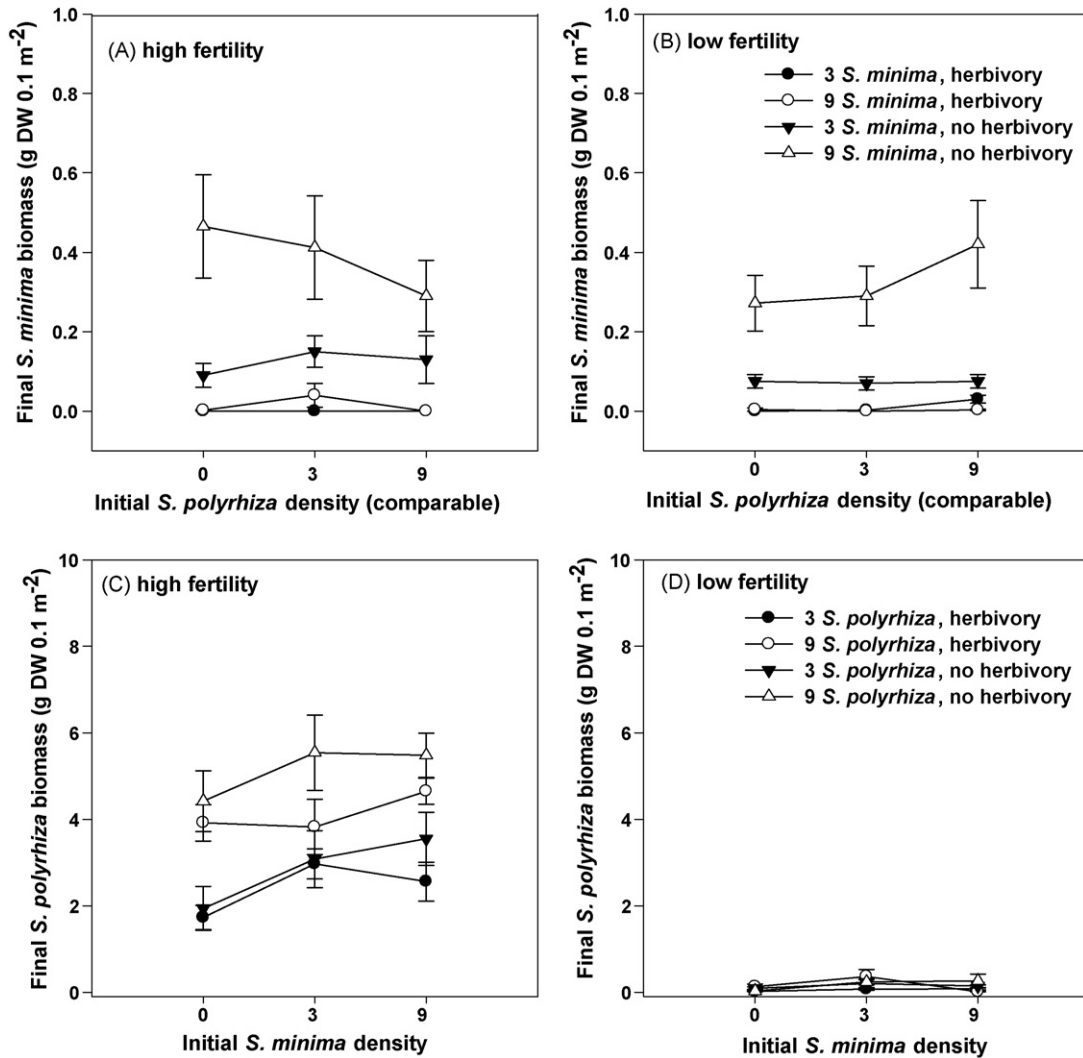


Fig. 1. Final biomass of plants as influenced by initial numbers of *S. minima* and *S. polyrhiza* (based on comparable biomass equivalents of *S. minima*), and herbivory on *S. minima*: (A) *S. minima* with high fertility; (B) *S. minima* with low fertility; (C) *S. polyrhiza* with high fertility; and (D) *S. polyrhiza* with low fertility. Error bars represent standard errors.

In many of the plant combinations, herbivory by *C. salvinia* extirpated salvinia regardless of fertility or competition from spirodela (Fig. 1). However, reductions or outright elimination of its presumed competitor did not result in concomitant increases in spirodela biomass (Fig. 1.). Under conditions of this experiment, differences of morphology and size allowed the smaller spirodela to crowd in and around salvinia, thereby occupying virtually every available space, in addition to forming multiple layers. Therefore, the reduction or elimination of salvinia by *C. salvinia* did not open significantly more space for colonization by spirodela.

Top-down and bottom-up influences can be system-specific even while varying in time and space (McIlraith et al., 1989). These data suggest that salvinia may dominate low fertility sites and spirodela more eutrophic sites. However, any dominance by salvinia will probably be short-lived should populations of *C. salvinia* increase. Likewise, it would be difficult to predict competitive outcomes without good information on spirodela herbivores, because the herbivore guild on spirodela is probably more complex than that on salvinia. These plant assemblages also experience dynamic and unpredictable disturbances from wind, currents, and the passage of animals, resulting in temporary gaps of open water that provide opportunities for spatial reordering of communities and plant dispersal. Ultimately, all of these factors coupled with the mosaic of wetland environments in Florida likely promote a continuum of competitive outcomes between salvinia and spirodela, thereby ensuring their continued coexistence.

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