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Herbivory alters competitive interactions between two invasive aquatic plants ☆

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Abstract

We compared the effect of herbivory by two congeneric specialist weevils (*Neochetina eichhorniae* and *Neochetina bruchi*) on competition between their host *Eichhornia crassipes* and another floating aquatic plant (*Pistia stratiotes*) by experimentally manipulating plant densities, presence of either or both herbivore species, and nutrient levels. Measurements of *E. crassipes* yield per original plant included biomass, clonal expansion, and flower production. Without herbivory, intraspecific competition among *E. crassipes* individuals was 41 times more intense than interspecific competition in terms of biomass yield. Herbivory shifted competitive outcomes, bringing intraspecific competition in line with interspecific competition. Both weevil species reduced *E. crassipes* biomass and flowering, but *N. bruchi* also lessened clonal expansion (rosette density) whereas *N. eichhorniae* did not. Nutrient limitation reduced plant performance but did not alter the pattern of competitive interactions. However, low nutrients moderated differences between weevil species such that both seemed equally damaging. We conclude that while herbivory directly and indirectly affected plant performance by altering competition between these two invasive plant species, the competitive response varied depending upon the herbivore species and availability of nutrients. The influence of herbivores on competitive interactions may thus be an important consideration for evaluating the invasive potential of exotic plant species as well as for predicting the potential efficacy of biological control agents, but interactions between herbivory, competitors, and nutrient availability create complexities that must be considered.
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1. Introduction

Competition and herbivory are both thought to be key factors in determining the structure and dynamics of plant communities (Crawley, 1983; Harper, 1977). Interspecific competition and herbivory can both lead to reductions in biomass, growth, reproduction, and other measures and components of fitness in plant species (Cipollini and Bergelson, 2002). For example, Center et al. (1999) showed that *Eichhornia crassipes* (Mart.)

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Solms. (Pontederiaceae) subjected to sustained herbivory in the field allocated proportionately less biomass to floral structures than plants less affected by herbivory. Additionally, competition and herbivory can, in theory, each act in a density-dependent manner, potentially regulating populations and leading to species coexistence and increased biological diversity (Coley and Barone, 1996; Connell et al., 1984; Parmesan, 2000). For these reasons, a large body of theoretical and empirical work has developed around these two phenomena. However, investigations into how competition and herbivory may interact to influence population dynamics and community level patterns have been few compared to studies of their separate effects.

Herbivores directly affect the species they consume, but they rarely "eat plants to extinction," and so may primarily influence the distribution and abundance of species by altering competitive interactions (Crawley, 1983). Herbivores potentially alter the outcome of competition either by causing greater damage to a dominant competitor or by causing a uniform level of damage among species, thereby enabling the more tolerant species to predominate (Louda et al., 1990). In the former case, the herbivore could either be a specialist on the dominant competitor species or could feed in a density-dependent manner, causing greater damage to the more abundant species. In the latter case, herbivory would act like a disturbance or a stress, with the more tolerant species increasing in abundance relative to less tolerant species in the presence of the stress or disturbance. The effect of herbivory on competitive interactions should thus depend on the degree to which the herbivory impacts a dominant competitor compared to a competitively inferior species. This differential effect of herbivory will in turn depend on (1) the preference of the herbivore for the dominant competitor, (2) the severity of damage to the dominant competitor by the herbivore, (3) the degree of density-dependence in the pattern of herbivore damage, and (4) the level of tolerance by the dominant competitor to herbivory. The above effects may further depend on natural enemies of the herbivores, phytopathogens, physiological and nutritional status of the plants, or other environmental factors.

It is necessary to manipulate both the level of herbivory as well as the competitive environment of the plant to fully explore the effects of herbivory on competitive interactions. Several previous studies have examined interactions between herbivory and competition by manipulating the presence or absence of these effects (Cottam et al., 1986; Maron, 1997; Maschinski and Whitham, 1989; McEvoy et al., 1993; Swank and Oechel, 1991). These studies have greatly increased our insight into interactions between competition and herbivory, but additional information may be gained by using more extensive competition designs. Specifically, hypothesis testing of the degree of density-depen-

dence in competitive interactions, herbivory, and their interactions is only possible if there are several density levels in the experiment. While the relative merits of various designs for competition experiments have been debated (Firbank and Watkinson, 1985; Joliffe, 2000; Sackville-Hamilton, 1994; Snaydon, 1991, 1994), it is now generally agreed that the most powerful and useful competition designs are those in which several density levels of two or more species are varied in a full factorial combination. Such factorial competition designs have been variously called addition series (Spitters, 1983), bivariate factorial (Snaydon, 1991), and response surface (Inouye, 2001) designs. Despite the benefits of such factorial designs, they have rarely been used to study interactions between competition and herbivory (but see Van et al., 1998, 1999).

In this study, we investigated how herbivory by two highly specialized congeneric weevil species (biological control agents of waterhyacinth, *E. crassipes*) influenced competitive interactions between two free-floating invasive aquatic plant species. In one experiment, we manipulated the density of each plant species and each insect species in a full factorial combination. In a second experiment, we combined a nutrient limitation treatment with herbivory treatments at a constant level of plant competition. Plants in the first experiment were space-limited whereas in the second experiment they were nutrient-limited. We measured plant performance as biomass and both clonal and sexual reproduction. These experiments were conducted to test the hypotheses that: (1) both competition and herbivory would reduce plant performance; (2) *E. crassipes*, which is known to be a dominant competitor in the field (Sutton, 1983; Tag El Seed, 1978), would outperform waterlettuce *Pistia stratiotes* L. (Araceae) in the absence of herbivores; (3) herbivory would alter the outcome of competition through differential impact on the dominant competitor; and (4) reduced nutrient levels would further enhance the impact of herbivory on competitive interactions by limiting the abilities of plants to compensate for herbivore damage. Analyses of variance were used to test for treatment effects and interactions, and data were fitted to linear inverse yield models to estimate competition parameters. Response surfaces were constructed to visualize the impact of herbivory across the range of competitive environments.

2. Methods and materials

2.1. Study species

2.1.1. Eichhornia crassipes (waterhyacinth)

Eichhornia crassipes, commonly known as waterhyacinth, was introduced from South America into North America during the late 19th century. It has since spread

to numerous tropical and subtropical areas of the world (Julien, 2001), often with devastating socio-economic and environmental consequences (Labrada, 1996; Mailu et al., 1999). The individual rosette is an erect, free-floating, stoloniferous, and perennial herb bearing a whorl of 6–10 sequentially produced, succulent leaves on a short, vertical stem (Center, 1987a). Individual plants (genets) produce clones of attached rosettes (ramets) that eventually become independent. The buoyant leaves vary in size and morphology according to growing conditions and the stage of colony development (Center et al., 1999). Leaves with bulbous petioles predominate in open water whereas attenuated elongate petioles are prevalent in dense stands. In the latter case, these elongate petioles support continuous leaf canopies held up to 1.5 m above the water surface. The plants produce copious numbers of seeds (Barrett, 1980) but populations increase mainly by vegetative means, through stolon elongation, from the differentiation of axillary meristems (Richards, 1982; Watson, 1984; Watson and Cook, 1982, 1987; Weber, 1950). The fragile stolons break easily enabling drifting rosettes to colonize new sites. More extensive accounts of the ecology and biological control of waterhyacinth can be found in Center and Spencer (1981) and Center et al. (2002).

2.1.2. Pistia stratiotes (waterlettuce)

Pistia stratiotes is a stoloniferous macrophyte that also forms mats of freely floating rosettes bearing several sequentially produced leaves. The rosettes exist singly or as interconnected clones. Like *E. crassipes*, seeds remain dormant in the sediments for prolonged durations, only germinating during periods of reduced water levels, on flotsam, or along shorelines. The shorter stature and more compact growth form of *P. stratiotes* places it at a competitive disadvantage relative to *E. crassipes* (Agami and Reddy, 1990; Sutton, 1983). Introduction of waterhyacinth-feeding insects appears to have reversed the outcome of competition in some cases, however, inasmuch as water bodies formerly dominated by waterhyacinth have since become dominated by waterlettuce (T.D. Center, personal observation). A more extensive account of the biology of waterlettuce can be found in Dray and Center (2002).

2.1.3. Neochetina eichhorniae and N. bruchi (Coleoptera: Curculionidae)

Semiaquatic weevils in the genus *Neochetina* use plants in the Pontederiaceae as developmental hosts. Center (1994) summarized the biologies of *N. eichhorniae* and *N. bruchi*, which both develop exclusively on *E. crassipes*. Adults are readily distinguished (DeLoach, 1975b; O'Brien, 1976; Warner, 1970), although larvae are less distinct. Females lay eggs in leaves and larvae burrow down to the petiole bases, where they often damage adjacent axillary buds (developing stolons),

which impairs clonal growth. Adult scraping of the leaf surface creates characteristic rectangular pits often causing the leaves to desiccate and curl (see Center et al., 1999; DeLoach and Cordo, 1983; Wright and Center, 1984). Chronic weevil infestations cause infested plants to be shorter in stature with smaller leaves, fewer offsets and flowers, lower tissue nutrient content, and reduced overall vigor than healthy plants (Center and Van, 1989; Heard and Winterton, 2000).

2.2. Experimental design

Stock cultures of *E. crassipes* and *P. stratiotes* were produced from plants collected at Lake Okeechobee, Florida, USA, during spring 2001. The plants were sprayed with insecticide, as needed, to eliminate insects. Bioassays done by feeding leaves from treated plants to adult weevils revealed no residual effects from the insecticide at the beginning of the study.

Adults of *N. eichhorniae* and *N. bruchi* were collected in western Broward County, Florida. Herbivory treatments consisted of either species alone or both species combined. *Eichhornia crassipes* plants from stock cultures were counted, then infested at rates of 2 pairs (2 ♂:2 ♀)/plant. These infested plants were placed in circular pools (235 cm diameter × 102 cm deep, water depth 72 cm) during mid-May. Those infested with *N. bruchi* were placed in one pool, those with *N. eichhorniae* in a second, and those with both herbivores in a third. One-third of the plants from each of the three groups placed into a fourth pool were periodically treated with insecticide to eliminate the weevils. This procedure evenly exposed all plants within an herbivory treatment to the same insect population. This had the added advantage of providing plants all with a similar history of herbivory-induced injury. It also provided plants containing all weevil life stages for use in the experiments so as to preclude any lag between introduction of the insects and manifestations of their effects. All pools were covered with screen and the plants were held in this condition for about two months to enable the insect population to develop.

For the experiments, mixtures of *E. crassipes* (dry weight 6.6 ± 0.4 g/plant) taken from the pools and *P. stratiotes* (dry weight 5.0 ± 0.4 g/plant) from stock cultures were placed into separate outdoor concrete tanks (0.8 m wide × 2.2 m long × 0.65 m deep) at the University of Florida's Research and Education Center in Fort Lauderdale, Broward County, Florida (26 °12′N, 80 °53′W), USA on 13 June 2001. The competition experiment consisted of factorial combinations of the two plant species within each herbivory treatment in a randomized complete block design. The eight *Eichhornia/Pistia* planting densities were 0:3, 0:9, 3:0, 3:3, 3:9, 9:0, 9:3, and 9:9 individual rosettes per tank. Four sets (one set for each herbivory treatment) of 8 tanks

comprised a block and three blocks were established, for a total of 96 tanks (surface area 1.76 m²/tank). The tanks were filled to a depth of 0.5 m (volume 0.9 m³) using pond water derived from the local aquifer [water quality described by Van and Steward (1986)]. Nutrients were supplied from 800 g of slow-release fertilizer per tank (Osmocote Plus 15-9-12 N:P:K, Southern 8-9 month formulation) in floating dispensers. Iron chelate (18 g Miller Iron Chelate DP 10% Fe) was added directly to the water. The tanks were covered with 7×5.5 strands/cm (18×14 strands/in.) mesh-window screen to exclude plant-feeding invertebrates.

Ten randomly selected plants, removed from the tanks to estimate initial plant weight, were replaced with plants randomly picked from the pools. Nutrients were supplied as in the stock cultures described above. One-meter-tall cages (window screen, as above) secured over each tank prevented escape of the weevils and contamination from outside sources.

The plants were harvested during 14–15 Aug. 2001, two months after the experiment was started. Numbers of both species and all *E. crassipes* inflorescences were counted. A subsample of 10 plants of each species, or all of the plants in cases where few plants remained, was analyzed gravimetrically for fresh weight after draining in cloth bags for at least 1 h and dry weight after drying at 60 °C for 30 days. Fresh weights for all of the remaining plants of each species from each tank were determined as above, and total dry weight was estimated based on the fresh:dry weight ratios for each species in each tank (regression of dry weight on fresh weight $r^2 = 0.974$, $P < 0.0001$, 70 *df*).

Weevils found were sorted according to sex and species, and counted. Females were dissected as described by Grodowitz et al. (1997) to ascertain their reproductive status. All weevils were further examined for entomopathogens, such as microsporidial spores, by inspecting body fluids and internal tissues with phase-contrast microscopy (40×).

To examine the effects of nutrient limitation at a constant level of competition, we conducted an experiment in which the presence and identity of herbivores was varied under differing nutrient conditions. Tanks were stocked with 3 *P. stratiotes* and 3 *E. crassipes* plants infested with *N. eichhorniae* alone, *N. bruchi* alone, or both species as described above ($n = 3$ replicates × 4 treatment combinations = 12). Each tank was fertilized on 20 June 2001 with 25 g of Osmocote Plus 15-9-12 N: P: K, Southern 8-9 month formulation (ca. 1 ppm N). All plants were harvested on 22 August 2001, counted, and weighed as before. The weevils were removed and examined as described above. These data were compared to the equivalent (3 *E. crassipes*:3 *P. stratiotes*) treatments from the preceding experiment, in which nutrient supply (>30 ppm N) was presumably not limiting (Reddy et al., 1989).

2.3. Analyses

Data were analyzed using SAS (1999). Analyses of variance (ANOVA) elucidated the effects of block, competition treatment, herbivore treatment, and their interactions on yield (per original rosette) as measured by final biomass and ramet abundance. Many treatments produced no inflorescences at all, which dictated against the use of ANOVA, so flowering data were analyzed using a series of Goodness-of-Fit tests (Sokal and Rohlf, 1981). These *G* tests examined the null hypothesis that there were no differences in flower production among treatments, so expected frequencies were calculated as the overall mean number of inflorescences per original plant. Some tests were constructed to enable partitioning of overall goodness of fit (G_t) into components including the heterogeneity *G* statistic (G_h), which is analogous to the interaction term of an ANOVA (Sokal and Rohlf, 1981). Some sample sizes were small ($n < 30$) so simple *G* values were adjusted using Williams' correction (G_{adj}) as recommended by Sokal and Rohlf (1981). However, adjusted *G* values are not additive, so Williams' correction was not applied to the ANOVA-like *G* tests (in which individual *G* values are summed and partitioned) (Sokal and Rohlf, 1981).

Data were also fitted to a linear inverse yield model within each herbivore treatment to derive competition coefficients (Pantone et al., 1989). In this model,

$$1/\bar{Y}_e = a_{e0} + a_{ee}d_e + a_{ep}d_p,$$

where $\bar{Y}_e$ represents the average *E. crassipes* yield per plant, d_e the planting density of *E. crassipes*, and d_p the planting density for *P. stratiotes*. The coefficients a_{ee} and a_{ep} measure intraspecific and interspecific competition, respectively, in terms of their effect on reciprocal *E. crassipes* yield. The ratio a_{ee}/a_{ep} measures the effects of intraspecific competition by *E. crassipes* on its own yield relative to the effects of interspecific competition by *P. stratiotes* on *E. crassipes* yield. Data on *P. stratiotes* yield, which was not directly affected by herbivory, are not presented.

3. Results

3.1. Herbivore intensities

Treatments effectively produced populations of each appropriate weevil species (Table 1). Visible signs of plant damage were not apparent in the control treatments, although some minor feeding occurred late in the study and a few weevils were recovered at harvest. Treatments with *N. bruchi* alone and *N. eichhorniae* alone remained pure cultures of each intended species. Weevil infestations became more intense in treatments with *N. bruchi* alone (0.69 ± 0.12 weevils/plant, mean ±

Table 1
Intensity (count/plant based on 10 plants/tank) of adult weevils (mean ± SE, $n = 3$) at the end of the study on *Eichhornia crassipes* (H) planted in varying mixtures with *Pistia stratiotes*[a]

Planting mixture	Weevil exposure treatment							
	None		Both Species		*N. bruchi* alone		*N. eichhorniae* alone	
	NE	NB	NE	NB	NE	NB	NE	NB
3H:0L	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.09	0.14 ± 0.03	0.00 ± 0.00	0.42 ± 0.37	0.23 ± 0.09	0.00 ± 0.00
3H:3L	0.00 ± 0.00	0.03 ± 0.03	0.17 ± 0.17	0.37 ± 0.27	0.00 ± 0.00	0.52 ± 0.18	0.37 ± 0.20	0.00 ± 0.00
3H:9L	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.08	0.25 ± 0.13	0.00 ± 0.00	0.71 ± 0.39	0.45 ± 0.26	0.00 ± 0.00
9H:0L	0.10 ± 0.10	0.07 ± 0.07	0.10 ± 0.06	0.13 ± 0.03	0.00 ± 0.00	0.71 ± 0.32	0.43 ± 0.26	0.00 ± 0.00
9H:3L	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.15	0.60 ± 0.31	0.00 ± 0.00	0.86 ± 0.14	0.33 ± 0.24	0.00 ± 0.00
9H:9L	0.00 ± 0.00	0.07 ± 0.07	0.05 ± 0.05	0.14 ± 0.14	0.00 ± 0.00	0.90 ± 0.47	0.57 ± 0.32	0.00 ± 0.00

[a] NE, *Neochetina eichhorniae*; NB, *Neochetina bruchi*.

SE) as opposed to those with *N. eichhorniae* alone ($0.40 ± 0.09$ weevils/plant) (paired t test, $t = 2.2$, $df = 17$, $P = 0.042$). Intensities of *N. bruchi* tended to be greater than *N. eichhorniae* in combined treatments ($0.27 ± 0.08$ vs. $0.14 ± 0.04$ weevils/plant; $t = 2.9$, 17 df, $P = 0.01$). Weevil intensities in tanks with both species averaged less (0.41 weevils/plant) than in those with *N. bruchi* alone ($0.69 ± 0.12$ weevils/plant, $t = 2.6$, 17 df, $P = 0.020$), but the same as those with *N. eichhorniae* alone. While some weevils showed signs of microsporidiosis, levels of infection were low [5 *N. eichhorniae* (3.3%) and 6 *N. bruchi* (1.9%) infected]. Nearly all *N. eichhorniae* females (92%) were parous with healthy ovaries, as compared to 62% of the *N. bruchi* females, but ovaries of all non-parous individuals were nulliparous indicating that they had recently emerged (Grodowitz et al., 1997). Hence, neither disease nor fecundity was a confounding factor.

3.2. Competition

Analysis of biomass yields of *E. crassipes* expressed as either fresh weight or dry weight produced similar results. So, to avoid redundancy, we restrict discussion to dry weight yield. Regression analysis revealed that, without herbivory, *E. crassipes* biomass production was strongly influenced by intraspecific but not by interspecific competition ($a_{ee} > 0$, but $a_{ep} \approx 0$; Table 2). In contrast, waterhyacinth clonal expansion (rosette density) was influenced by both intra- and interspecific competition (Table 2). The competition ratio (a_{ee}/a_{ep}) for *E. crassipes* biomass yield indicated that intraspecific competition was 41 times stronger than interspecific competition. This can be understood to mean that 41 *P. stratiotes* plants would be required to reduce *E. crassipes* biomass yield by an amount equivalent to that caused by the addition of a single *E. crassipes* plant. This disparity was less pronounced when yield was measured in terms of clonal expansion (rosette density), but intraspecific competition remained 3-fold stronger (Table 2).

3.3. Herbivory

Eichhornia crassipes grew well and flowered abundantly in control (no herbivory) treatments (Fig. 1). Herbivory reduced biomass production, clonal expansion, and flowering but the effects differed depending upon the yield parameter being considered. Biomass yield declined due to herbivory, with *N. bruchi* inducing greater reductions than *N. eichhorniae* (Fig. 1A) but both weevil species restricted flowering by similar amounts (Fig. 1C). In contrast to both of these

Table 2
Multiple regression analyses (using the inverse linear model) testing the hypotheses that initial densities of *P. stratiotes* and *E. crassipes* affect dry *E. crassipes* biomass yield (kg) or rosette production with and without the influence of either or both weevil species (*N. eichhorniae* and/or *N. bruchi*)

Variable	Treatment	Intercept	a_{ee}	a_{ep}	R^2	F value (P)	a_{ee}/a_{ep}	t value (P)[*]
Dry weight (kg)	Control	1.966	1.264[a]	0.031	0.53	8.4 (0.004)	41.17	3.12 (0.007)
	N. bruchi	−61.732	14.963	18.988[a]	0.36	4.2 (0.036)	0.79	0.33 (0.745)
	N. eichhorniae	4.518	1.117[a]	0.783[a]	0.40	5.0 (0.022)	1.43	0.55 (0.589)
	Both species	−132.44	21.246	33.828[a]	0.51	7.9 (0.004)	0.63	0.83 (0.421)
Rosettes	Control	−0.009	0.011[a]	0.004[a]	0.87	48.7 (<0.001)	3.00	4.74 (<0.001)
	N. bruchi	−0.544	0.086	0.162[a]	0.39	4.8 (0.025)	0.53	0.83 (0.420)
	N. eichhorniae	−0.012	0.012[a]	0.008[a]	0.65	14.0 (<0.001)	1.50	1.10 (0.289)
	Both species	−0.699	0.098	0.218[a]	0.46	6.5 (0.009)	0.45	1.16 (0.265)

[a] Coefficient significantly different from 0 at $P \leqslant 0.056$.
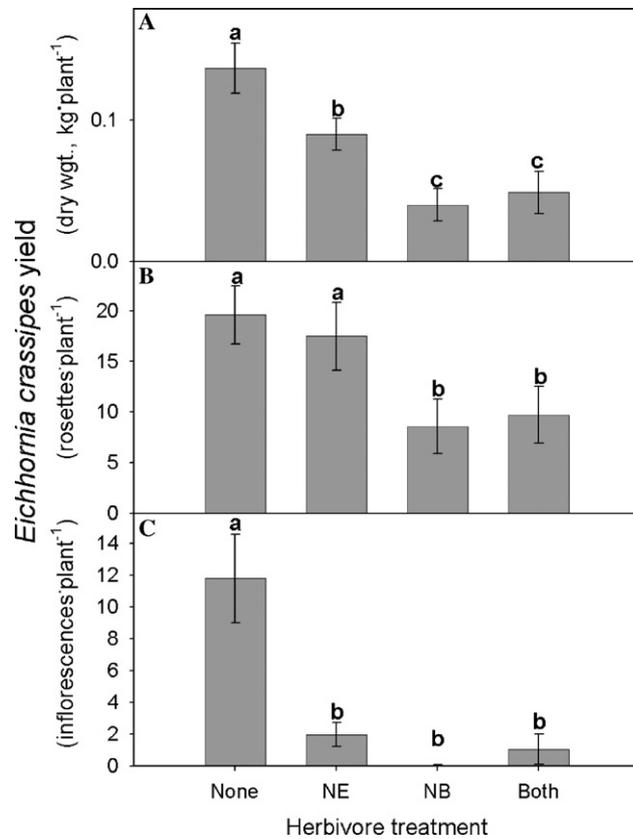[*] Tests the hypothesis that $a_{ee} = a_{ep}$.

Fig. 1. Herbivory by the monophagous weevils *Neochetina eichhorniae* and *N. bruchi* influenced *Eichhornia crassipes* yield per initial stock plant as measured by (A) dry weight biomass, (B) rosette production, and (C) inflorescence production. Means labeled with the same letter do not differ statistically ($P > 0.05$).

outcomes, clonal expansion (rosette density) was suppressed by *N. bruchi*, but not by *N. eichhorniae* (Fig. 1B). The two weevil species together ("Both" in Fig. 1), produced effects similar to *N. bruchi* alone, despite lower weevil intensities (0.41 vs. 0.69 weevils/plant) in these treatments (Table 1).

3.4. Interactions between herbivory and competition

Herbivory and competition influenced one another, but sometimes in subtle ways that were not manifested as simple interactions (Table 3). For example, analysis of variance indicated that the effect of intraspecific competition on *E. crassipes* biomass yield was similar across all herbivory treatments (W × H in Table 3). Yet individual contrasts (not shown) within this interaction indicated that biomass was suppressed with modest levels of intraspecific competition and the presence of both weevil species, but that intense intraspecific competition amplified biomass suppression to the point of obscuring the interaction ($F = 4.25$, $P = 0.045$; Fig. 2). In contrast, herbivory effects on clonal expansion were consistent across levels of intraspecific competition inasmuch as these two variables did not interact (W × H under rosettes in Table 3). But herbivory effects did depend upon
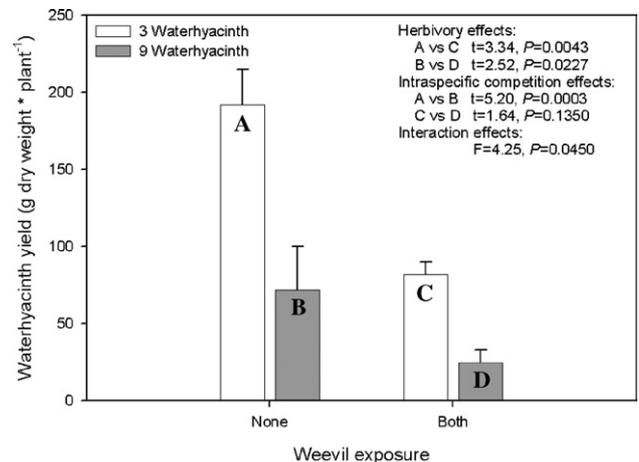

Fig. 2. Herbivory and intraspecific competition combine to suppress waterhyacinth biomass yield more substantially than either does alone. Bars represent means (±SE).

Table 3
Summary of analyses of variance testing the effects of *Eichhornia crassipes* (E) and *Pistia stratiotes* (P) planting densities, and weevil exposures (W), on *Eichhornia crassipes* yield (per initial plant) based on biomass (dry weight) and clonal expansion (numbers of rosettes)

Source	df	Dry weight (kg)		Rosettes	
		MS	F value	MS	F value
Model	25	36568.5	4.80**	1.46	3.38**
Block	2	20988.5	2.76	1.25	2.91
Weevils (W)	3	68503.5	9.00**	2.30	5.33**
E. crassipes (E)	1	60314.5	7.92**	1.75	4.07*
P. stratiotes (P)	2	97473.1	12.80**	5.18	12.01**
W × H	3	16514.7	2.17	0.36	0.83
W × P	6	35759.3	4.70**	1.61	3.74**
E × P	2	30328.6	3.98*	1.05	2.44
W × E × P	8	14454.0	1.90	0.34	0.80
Residual	46	7614.5	—	0.43	—

* Probability of a greater *F* value <0.05, <0.01.
** Probability of a greater *F* value <0.01.

the level of interspecific competition (W × P in Table 3). These numerous interactions influenced both biomass yield and clonal expansion (rosette density). The individual contrasts showed that *N. bruchi* reduced both of these yield variables more than *N. eichhorniae*, and that interspecific competition magnified this difference (biomass: $F = 4.34$, $P = 0.0426$; rosettes: $F = 5.82$, $P = 0.0199$).

Parameters of the inverse linear yield model (Table 2) showed parity between intraspecific competition and interspecific competition, as measured by biomass production, for *E. crassipes* subjected to herbivory. None of the competition ratios (a_{ee}/a_{ep}) statistically deviated from unity when either or both herbivores were present. However, intraspecific competition coefficients (a_{ee}) were not significant in cases where *N. bruchi* or both weevils were present, whereas interspecific competition coefficients (a_{ep}) consistently were. In contrast,

only intraspecific competition affected biomass yield when weevils were not present (i.e., in the controls), whereas both intraspecific and interspecific competition influenced clonal expansion (rosette yield). Interestingly, in the case of *N. eichhorniae*, both coefficients were significant for both yield variables. This was similar to the control in terms of rosette yield but, unlike the control, indicated that in terms of biomass yield herbivory by this species led to heightened interspecific competition.

The response surface graphs (Figs. 3 and 4) illustrate the effects of each herbivore treatment on the outcome of competition. In the absence of herbivory (Figs. 3A and 4A), *E. crassipes* yield depended almost exclusively on intraspecific competition, with negligible effect from *P. stratiotes*. *Neochetina eichhorniae* changed the pattern somewhat (Figs. 3B and 4B), as interspecific competition fell in line with intraspecific competition, but the overall
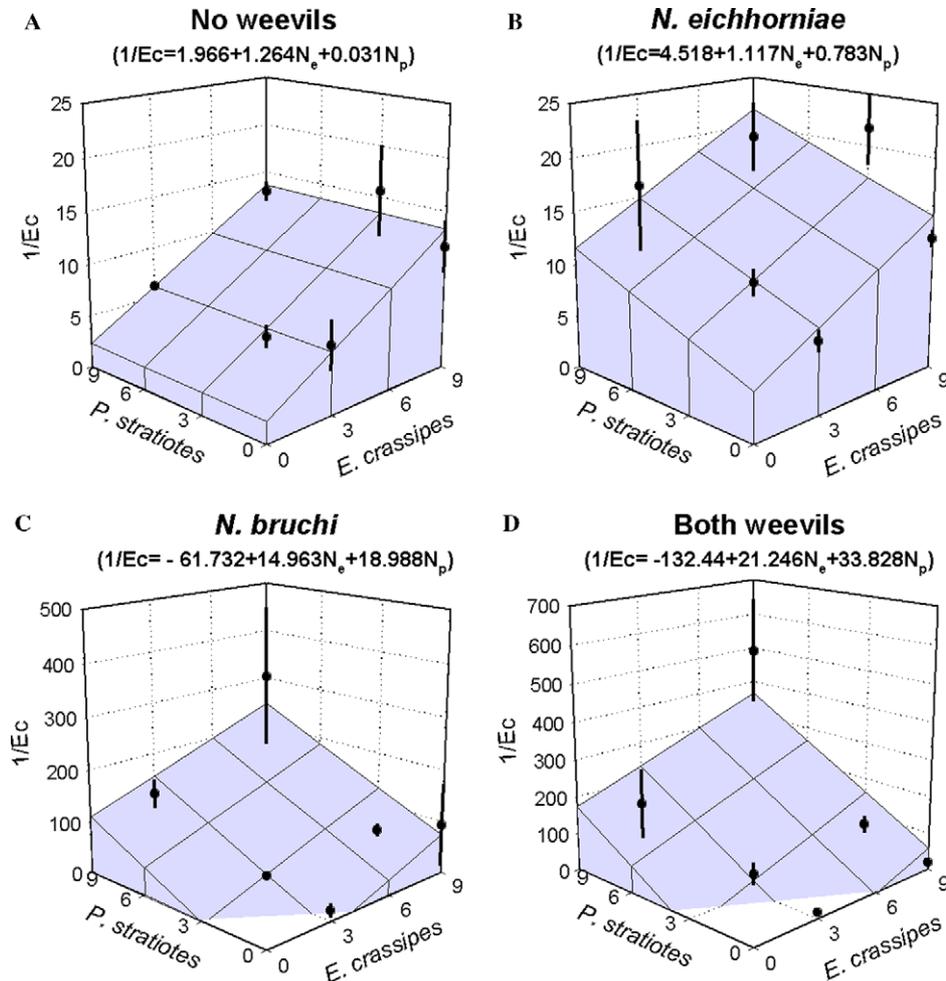

Fig. 3. Multiple regression planes demonstrating the effects of exposure to either or both species of weevil and intraspecific and interspecific plant competition on the reciprocal of the mean dry weight yield harvested per initial *Eichhornia crassipes* plant (1/Ec). Graph A represents the control without weevils, B, C, and D shows changes that result when competition is altered by *N. eichhorniae* alone, *N. bruchi* alone, or both together, respectively. Points represent means adjusted to remove block effects and vertical lines represent standard errors. Values on *X* and *Y* axes represent initial *E. crassipes* and *Pistia stratiotes* planting densities and the *Z*-axis represents the inverse yield.
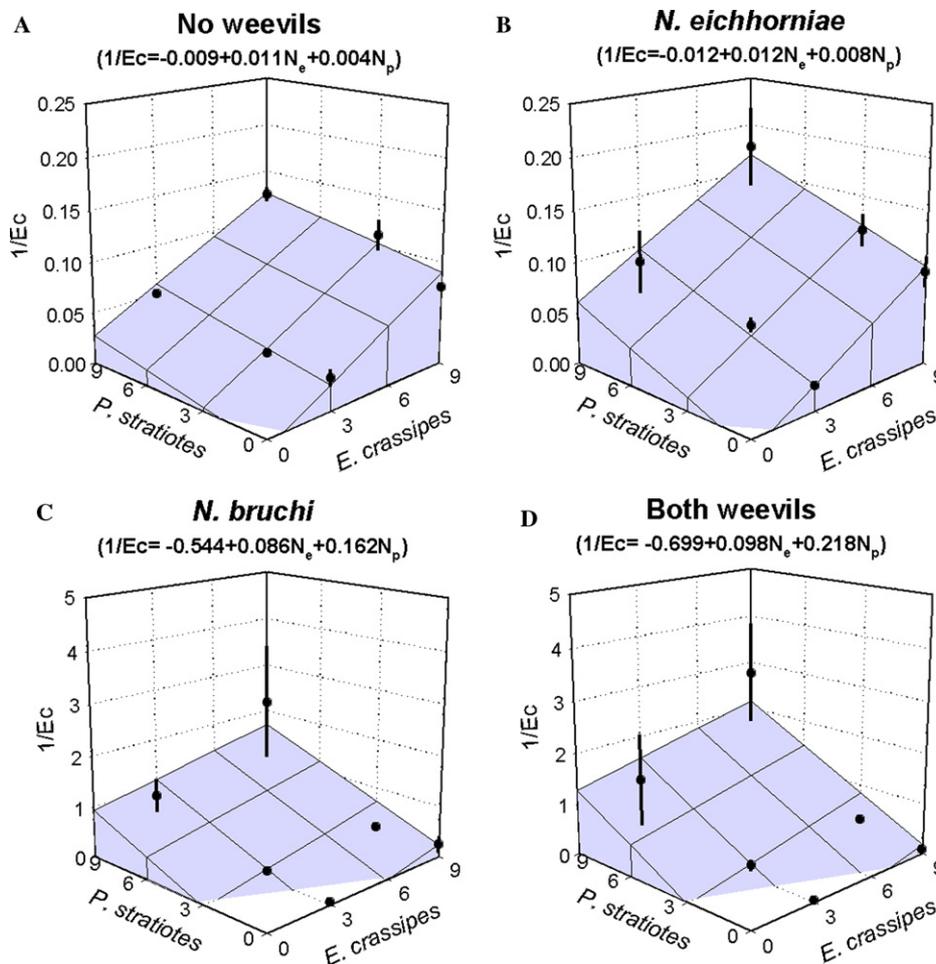
Fig. 4. Multiple regression planes demonstrating the effects of exposure to either or both species of weevil and intraspecific and interspecific plant competition on the reciprocal of the number of clonal offsets (rosettes) per *Eichhornia crassipes* plant (1/Ec). Labels are as described in Fig. 3.

pattern for rosette yield did not change greatly. However, even in this case, the intensity of intraspecific relative to interspecific competition was reduced from 41.2 to about 1.4 for biomass yield and from 3.0 to 1.5 for rosette yield. In contrast, *N. bruchi* substantially shifted the competition response surfaces for both yield variables (Figs. 3C and 4C). In the case of rosette yield, the intraspecific competition coefficient was about half of the interspecific competition coefficient. The effect of both weevil species together approximated that of *N. bruchi* alone but the ratio of intraspecific to interspecific competition was further reduced. In the most extreme case (fresh weight yield), a single *P. stratiotes* plant became competitively equivalent to about five *E. crassipes* plants in terms of its effect on *E. crassipes* yield (data not shown).

3.5. Nutrient effects

Fig. 5 compares the effects of herbivory treatments on waterhyacinth yield under conditions of low or high fertility when planted in mixtures of 3 *P. stratiotes* and 3 *E.*

crassipes plants. The weevils reduced clonal expansion (rosette density) relative to the control in all treatments. Lower nutrients reduced clonal expansion within all herbivory treatments except for that with both weevil species. Basically, neither *N. bruchi* alone or together with *N. eichhorniae* reduced yield more than *N. eichhorniae* alone in low nutrient conditions, inasmuch as the differences were not statistically supported, but all herbivore treatments reduced yield relative to the untreated controls.

Effects on biomass yield were similar except that no differences were seen between fertility levels in the treatments with *N. bruchi* alone or both weevil species together. Very little growth occurred in any low fertility treatments, and exposure to herbivory further reduced biomass yield.

Both weevil exposure and low fertility levels greatly reduced flower production. Most of the flowers were produced by plants grown with high nutrients that were not subjected to herbivory. Almost no flowers were produced by plants exposed to herbivory, regardless of weevil species.
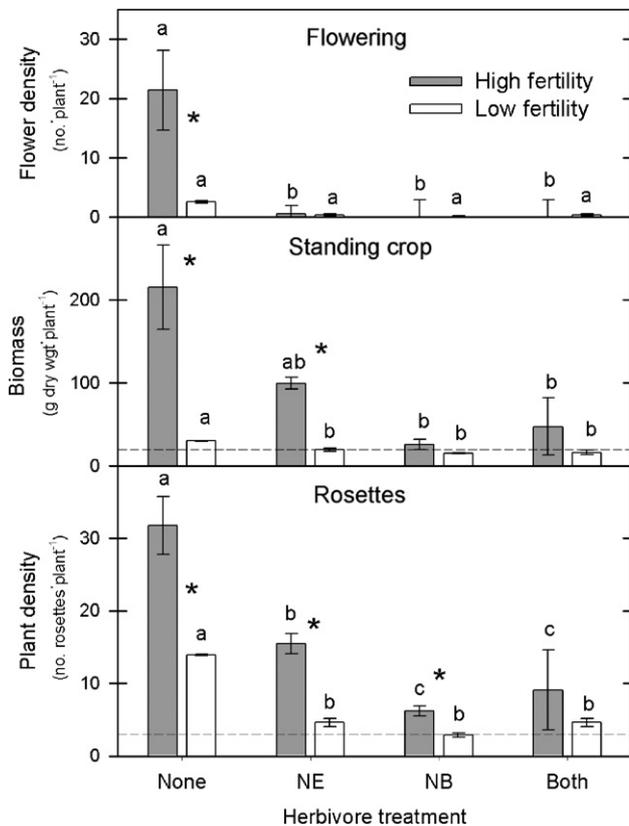
Fig. 5. Effects of high and low nutrients on *Eichhornia crassipes* yields per plant for plants not exposed to weevils ('None') or infested with *Neochetina eichhorniae* alone ('NE'), *N. bruchi* alone ('NB'), or both together ('Both') in terms of numbers of plants, biomass, and inflorescences in tanks with an initial mixture of 3 *E. crassipes* and 3 *Pistia stratiotes*. The horizontal dashed lines represent initial values. Lower case letters compare means among weevil exposures (horizontally, same colored bars). Asterisks compare between fertility levels within a weevil exposure (different colored bars). Means (bars) and standard errors of the means (lines) are presented. Means with different letters or denoted with an asterisk are significantly different at *P* = 0.05.

4. Discussion

4.1. Competition

Competition theory states that two ecologically similar species cannot indefinitely coexist on the same limiting resource (Gause, 1934; Lack, 1944; Hutchinson, 1957; Hardin, 1960; [cited in Ricklefs, 1990]). Habitat space represents a particularly serious limiting resource for terrestrial plants because individuals are immobile. Floating species are somewhat unique, however, inasmuch as they passively move, often by fragmenting, and thereby escape the spatial constraints that lead to competition (Room, 1983).

Eichhornia crassipes is an aggressive, floating, and aquatic weed (Little, 1965) whose structural architecture normally confers a competitive advantage over another floating weed, *P. stratiotes*, when the two are in a con-

fined space and freed from suppressive biotic agents. In the present study, *E. crassipes* was a strong competitor in the absence of herbivory in terms of both intraspecific and interspecific competition. In contrast, neither *E. crassipes* nor *P. stratiotes* yield (data not presented) was affected by *P. stratiotes* density, so *P. stratiotes* was a much weaker competitor. These results accord well with observations that *E. crassipes* replaces *P. stratiotes* where they are adventive and their distributions overlap (Gay, 1958; Sutton, 1983) and are consistent with experimental findings of other researchers (Agami and Reddy, 1990; Tag El Seed, 1978).

4.2. Herbivory

Herbivory reduced *E. crassipes* performance as measured by biomass production, clonal expansion, and flowering. One weevil species, *N. bruchi*, strongly depressed plant performance, whereas suppression by *N. eichhorniae* was less. This agrees with findings by Bashir et al. (1984) and supports predictions made by DeLoach (1975a) based upon the shorter generation time and the faster rate of increase of *N. bruchi* (DeLoach and Cordo, 1976a,b). But, in contrast to this prediction and to the results of the present study, *N. eichhorniae* has more often been credited with reducing infestations of *E. crassipes* in many areas of the world (Ajuonu et al., 2003; Bashir [sic] and Bennett, 1985; Center, 1987b; Center and Durden, 1986; Cofrancesco et al., 1985; Goyer and Stark, 1984; Jayanth, 1987; Julien and Orapa, 1999; Wright, 1981; but see DeLoach and Cordo, 1983 for an example of successful control using *N. bruchi*). Furthermore, *N. eichhorniae* has become more abundant and widely distributed in Florida (Center and Dray, 1992; Center et al., 1999). Thus, field observations on the performance of these two weevils as biological control agents seem to vary from the aforementioned predictions. This serves to highlight the difficulties likely to be encountered when attempting to predict the efficacy of weed biological control agents as is often advocated (McEvoy and Coombs, 1999; Myers, 1985).

4.3. Nutrient effects

The overall pattern of herbivore effect did not change between the two nutrient regimes but nutrient limitation reduced biomass yield, clonal expansion, and flowering masking differences between *N. eichhorniae* and *N. bruchi*. We anticipated, based on the study by Heard and Winterton (2000), that nutrient levels would differentially influence the effectiveness of the two weevil species. This proved to be true in one case inasmuch as *N. bruchi* affected *E. crassipes* yield more than *N. eichhorniae* in high fertility regimes, but the effects were similar under the low nutrient regime. We attribute this to the inability of the

plants to escape herbivory via a numerical response in the latter circumstance. Even though biomass production remained low, the plants not subjected to herbivory produced numerous rosettes, whereas those subjected to herbivory were less able to do so. Thus, the ability of the plants to escape by fragmentation and drifting may relate to their ability to produce vegetative propagules. Also, these results suggest that herbivory reduces the ecological amplitude of *E. crassipes*, making it less able to persist in marginal (i.e., low nutrient) habitats.

The evenness of effect regardless of weevil species may be related to the greater need of *N. bruchi* for nitrogen-rich tissues (Heard and Winterton, 2000). Preliminary data indicate that *N. bruchi* populations respond numerically to increased nitrogen levels whereas *N. eichhorniae* responds weakly only above a relatively high threshold (T.D. Center, unpublished data). Neither species produces large populations when nutrient levels are low. This suggests that their effects on plant competition should be examined across a broader range of nutrient concentrations.

In our main study, nutrients were quite high (nitrate-N >30 ppm) in order to avoid nutrient limitation. This might have biased results in favor of *N. bruchi*. Some data suggest that *N. bruchi* performs better on *E. crassipes* grown under high nutrient conditions because its higher nitrogen requirement enables it to produce larger populations by maintaining higher reproductive rates and thereby inflict more damage on the plants (Heard and Winterton, 2000). Weevil intensities (based on counts per plant) were, in fact, generally higher for *N. bruchi* than for *N. eichhorniae*. However, this may have been an artifact of resource availability. The greater impact to *E. crassipes* by *N. bruchi* limited the amount of biomass available to support population growth, so higher intensities might merely reflect the accumulation of *N. bruchi* adults on fewer plants rather than higher reproductive rates.

4.4. Interactions between herbivory and competition

Previous work has suggested that herbivory should alter the outcome of competition if there is a differential impact on the dominant competitor (Louda et al., 1990). Our results showed that herbivory indeed altered competitive outcomes between these two invasive aquatic plants. This finding is consistent with other studies showing that insect herbivory (Cottam et al., 1986; Friedli and Bacher, 2001; Norris, 1997), mammalian herbivory (Swank and Oechel, 1991; van der Wal et al., 2000), mechanical clipping (Alexander and Thompson, 1982; Hendon and Briske, 2002), and pathogens (Carsten et al., 2001) can alter the magnitude and/or outcome of competition. However, other studies have failed to detect an interaction between herbivory and competition (Fowler, 2002; Frost and Rydin, 1997; Maron, 1997).

In the present study, one weevil species, *N. bruchi*, effectively neutralized the strong intrinsic competitive advantage that *E. crassipes* held over *P. stratiotes*. This effect was evident across all measures of yield (flowers, clonal offsets, and biomass) suggesting that *N. bruchi* should be an effective control agent. The level of suppression by both species of weevils was enhanced by the presence of the competing plant species. The more variable effects of *N. eichhorniae* were evinced by reduced biomass more than by reduced flowering or clonal expansion. Plants, then, would more likely avoid suppression from *N. eichhorniae* because of their ability to continue to produce propagules, which would increase their likelihood of escape by drifting away from weevil-infested neighbors. Predator satiation might also be a factor inasmuch as *N. eichhorniae*, by virtue of lower egg production (DeLoach and Cordo, 1976b; but see Center, 1994), might be less capable of numerically responding to rapidly increasing plant populations. Flowering, in high nutrient situations where herbivory was not a factor, increased in response to interspecific competition but was reduced by intraspecific competition and herbivory. This suggests that *E. crassipes* responds to space limitation by increased sexual reproduction when growing conditions are otherwise suitable but abandons this strategy when stressed.

These weevils were introduced into the United States to control *E. crassipes* during the early 1970s, and have since become abundant and widely distributed (Center et al., 1999). However, the landscape-scale reductions in *E. crassipes* acreage that resulted (e.g., Cofrancesco et al., 1985) have been attributed to environmental factors (e.g., Haller, 1996) without consideration that such factors may be irrelevant in the absence of herbivory. Burger and Louda (1994) emphasized the importance of environmental context when evaluating plant performance and advised against evaluations of herbivory without consideration of the competitive and physical environment of the plant. Clearly, in the case of waterhyacinth, herbivore load, nutrient status, and the competitive environment are all important.

The effect of herbivory on competitive interactions found in this study explains patterns observed in the field. *Pistia stratiotes* replaced *E. crassipes* in Florida in many areas after specialist insects were introduced to control the latter species (Center, T.D., personal observation). This often occurred in conjunction with herbicidal control. Herbicidal control rarely succeeds in completely eliminating either *E. crassipes* or *P. stratiotes*. However, weevils often converge on the few remaining *E. crassipes* plants, subjecting them to intense herbivory (Center et al., 1999) and causing them to become less competitive. *Pistia stratiotes* then assumes the competitive advantage. As a result, sites formerly dominated by *E. crassipes* have become occupied by the less aggressive *P. stratiotes*.

The interaction between two species should be less stable as intra- and interspecific competition approach parity (Hastings, 1997; Maynard Smith, 1974). Herbivory then, by forcing competition towards parity, should lead to lower stability. This seemed to be true in the present study wherein lessened stability was reflected by increased variability when herbivores were present (i.e., the competition models explained less of the total variation).

These results have practical applications. A goal of biological control programs is to develop parsimonious biological control systems that pose minimal risk to non-target organisms while providing potent control (McEvoy and Coombs, 1999). Parsimony involves releasing the fewest possible species needed to provide adequate control, which necessitates choosing not just the safest, but also the most effective, agents. Various systems have been proposed to rate the efficacy of these agents prior to release, one of which has been applied to *E. crassipes* biological control agents (DeLoach, 1975a). This study supports DeLoach's (1975a) ranking by suggesting that *N. bruchi* should be more effective than *N. eichhorniae*.

A "parsimonious biological control system," then, would advocate release of only *N. bruchi*, because it performed better alone than when combined with *N. eichhorniae*. However, caution is advised. These results apply only under a specific set of conditions and may not be universally applicable. For example, high nutrient concentrations, as in our experiments, are likely to favor *N. bruchi* over *N. eichhorniae* (Center and Dray, 1992; Heard and Winterton, 2000; Jamil and Jyothi, 1988) and do not represent the range of conditions expected in most aquatic environments. Even though the general pattern seemed similar in low nutrient conditions, differences between the two weevil species were not apparent. Despite the seemingly greater impact from *N. bruchi*, it is the rarer of the two species in the field (Center and Dray, 1992; Center et al., 1999), and successful control has more often been attributed to *N. eichhorniae* (Julien and Griffiths, 1998). Attempts to develop "parsimonious control systems" then, could require long and costly evaluations that mistakenly reject potentially effective agents. However, competition studies could be used to detect subtle effects of candidate agents that might otherwise go unnoticed. For example, such experiments have recently demonstrated that a sap-feeding mirid (*Eccritotarsus catarinensis* (Carvalho), Hemiptera: Miridae) did indeed impact the ability of *E. crassipes* to compete with *P. stratiotes* despite the lack of obvious plant damage (Coetzee et al., 2005).

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