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Herbivory by Biological Control Agents Improves Herbicidal Control of Waterhyacinth (*Eichhornia crassipes*)

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Classical biological control of waterhyacinth is difficult to evaluate against the backdrop of active herbicide programs. Two experiments evaluated the additive impact of herbivory by two biological control agents with three different rates of 2,4-D on waterhyacinth growth and development in outdoor concrete mesocosms. The herbicide 2,4-D was applied at three rates: (1) control (no herbicide), (2) reduced (2.1 kg ai ha^{-1}), and (3) operational (4.3 kg ai ha^{-1}). Biomass of waterhyacinth populations was reduced by 16.9% by biological control only, 10.5% by the reduced rate of herbicide alone, 44.6% by the operational rate, and 97.3% and 99.9% by the combination of biological control and the reduced and operational rates of herbicides, respectively. These results quantified the relative contributions of both tactics to waterhyacinth management and posit the question of whether further reductions in 2,4-D rates are possible without sacrificing efficacy.

Nomenclature: 2,4-D; waterhyacinth, *Eichhornia crassipes* (Mart.) Solms.

Key words: Biological control, integrated control, *Megamelus scutellaris*, *Neochetina eichhorniae*.

Waterhyacinth [*Eichhornia crassipes* (Mart.) Solms] has been a challenging threat to freshwater drainages in the southern and western United States since the late 1880s. This species' rapid growth rate and mobility frustrated early attempts to physically remove it from water bodies (Wunderlich 1967). It was not until the development of phenoxy herbicides like 2,4-D in 1942 that an efficient and cost-effective tactic provided a way to reduce the plant to background levels using a maintenance-level approach (Hildebrand 1946). Originally defined in Florida as "a method for the control of non-indigenous aquatic plants in which control techniques are utilized in a coordinated manner on a continuous basis in order to maintain the plant population at the lowest feasible level as determined by the department," maintenance control for *E. crassipes* has become a herbicide-centric approach that has reduced the impact of this weed in Florida (Schardt 1997: 233). While this approach kills plants and reduces populations temporarily, it does not fundamentally change or stress the plants; when spraying stops, populations rebound rapidly, so the sustainability of maintenance control is irretrievably linked to the maintenance of budgets that support these programs. In Florida, more than 18,210 ha of *E. crassipes* and waterlettuce (*Pistia stratiotes* L.) were sprayed in 2014–2015 in public waters at a cost of more than $5 million (Phillips 2015).

Attempts to transform or permanently weaken the plants were pursued using classical biological control, wherein programs in the 1960s and 1970s identified, developed, and released three insect species in the United States, namely *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), *Neochetina bruchi* Hustache (Coleoptera: Curculionidae), and *Niphograpta albiguttalis* (Warren) (Lepidoptera: Crambidae) (Center et al. 2002; Perkins 1973). A fourth species, *Megamelus scutellaris* (Berg) (Hemiptera: Delphacidae) was released in 2010; it is now established in Florida (Tipping et al. 2014b). Although these biological control agents have reduced many of the more invasive qualities of this plant by slowing vegetative growth and significantly reducing seed production, surface coverage in the field remains unacceptably high in many areas (Tipping et al. 2014a).

Maintenance control as currently practiced in Florida does not take advantage of these biological investments, because spraying indirectly kills the sessile larval stages of the

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Management Implications

Combining two weed management tactics, biological and chemical, suppressed waterhyacinth more than either tactic used individually. Plants attacked by two biological control agents, *Neochetina eichhorniae* and *Megamelus scutellaris*, were unable to regrow as readily following applications of 2,4-D at two rates, a reduced rate and a higher operational rate. Herbivory by the insects likely weakened the plants to the point that the reduced rate of herbicide was as effective as the operational rate. This outcome may indicate that further reductions in herbicide rates are possible without sacrificing efficacy. A simple logistic model predicted that the suppressive activities of the insects reduces the number of herbicide re-treatments needed from five in a year to just two or a 60% reduction. Depending upon the herbicides used, this could add up to a considerable savings every year in places like Florida. In addition, the pattern of spraying may increase the effect of the insects by providing internal refuges within sprayed mats whereby insect attack would be more damaging to any remaining plants through increased rates of attack.

first three introduced species. Although rarely appreciated, the suppressive activities of the biological control agents have likely made chemical applications more effective, because the plants are weakened by herbivory (Center et al. 1999). The adult stages of both *Neochetina* species can survive exposure to the most commonly used herbicides, but certain types of adjuvants cause significant mortality (Haag 1986). The latest agent developed, *M. scutellaris*, was selected, in part, because all stages feed externally, and thus immatures would not be killed along with the plant when sprayed (Tipping et al. 2011). The direct effect of herbicides and adjuvants on this species has yet to be determined. In addition to the complete loss of immature stages, the unpredictable oscillations of weed populations caused by regular spraying inhibit insect populations from increasing to useful densities (Center et al. 1999). The challenge is to develop actively integrated programs that maximize the impact of these two tactics, as well as other broader actions like improving water quality, to more sustainably manage this plant in the future.

The objective of this research was to quantify the relative importance of some of the biological control agents to successfully managing *E. crassipes* with herbicides, with a longer range goal of developing a more balanced integrated weed management approach to reduce herbicide inputs into freshwater systems.

Materials and Methods

Testing was conducted at the USDA-ARS Invasive Plant Research Laboratory (IPRL) located in Davie, FL (26.084769 N, –80.2400703 W), in outdoor, unscreened concrete mesocosms filled with well water (1.6 m^2 surface area, ca. 868 L in volume). The experimental plant populations were initiated with five uninfested *E. crassipes* plants from cultures grown at IPRL that were weighed to obtain fresh weight biomass and then placed into the mesocosms and allowed to grow and multiply until 100% of the surface was covered. Each mesocosm received a mix of 300 g of slow-release 18-5-12 fertilizer plus 18 g of iron applied at the beginning of and midway through each trial. Aquashade (Lonza, Basel, Switzerland) was added as a dye once at labeled rates at the beginning of each trial to reduce algae. Trial 1 was started on July 2, 2013, subsampled on September 10, 2013, and harvested on January 28, 2014. Trial 2 was started on July 7, 2014, subsampled on September 9, 2014, and harvested on February 9, 2015.

The experimental design was a two by three factorial arranged in a completely randomized design with two insect treatments, three herbicide treatments, and five replications. Insect treatments were either (1) a control treatment in which plants were sprayed regularly with insecticides (acephate 0.07% ai or bifenthrin 0.01% ai) until wet to eliminate the biological control agents or (2) an insect treatment in which biological control agents were added periodically with no confinement to the *E. crassipes* growing in the mesocosms. Neither insecticide had negative effects on the growth of waterhyacinth in preliminary tests. The two agents used were *N. eichhorniae* and *M. scutellaris*. The herbicide treatments were (1) a control treatment in which the plants were sprayed with water, (2) a reduced rate of herbicide treatment in which the equivalent of 2.1 kg ha^{-1} of 2,4-D was applied, and (3) an operational rate of herbicide treatment in which 4.2 kg ha^{-1} of 2,4-D was applied. The herbicide used was WeeDestroy® AM40 (Nufarm Americas, Burr Ridge, IL), which contained 46.8% 2,4-D dimethylamine salt plus surface and sequestering agents to decrease volatility and increase solubility. The herbicides were applied using a backpack sprayer delivering a volume of 72 L ha^{-1} through a fan-tip nozzle. The equivalents of 3,741.6 L ha^{-1} and 935.4 L ha^{-1} of water were used as diluent in the first and second trials, respectively. The volume of diluent was reduced in Trial 2 after consultations with managers to more closely match field applications. A portable spray booth was placed around each mesocosm before application to eliminate drift. Herbicide applications were conducted on November 7, 2013, in Trial 1 and November 7, 2014, in Trial 2 after *E. crassipes* had achieved 100% coverage within the mesocosms.

The insect treatments in Trial 1 received a total of 275 *M. scutellaris* and 87 *N. eichhorniae* in each mesocosm on 14 separate occasions, usually every 7 to 14 d. Although the goal was to mimic insect densities found in the field (PWT, unpublished data), densities remained lower than desired, perhaps through increased emigration from the uncaged tanks. More insects were released more frequently during Trial 2, namely 385 *M. scutellaris* and 171 *N. eichhorniae* on

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37 occasions, usually every 5 to 7 d. The changes in methodology in Trial 2 succeeded in increasing insect densities that were comparable to field densities (PWT, unpublished data). Insect releases in both trials commenced within 3 wk of initiating the plant populations in the tanks. All insects were collected from rearing tanks at IPRL and released at sex ratios of approximately 50:50.

Plant populations were assessed weekly pre- and postspray for the number of flowers. One destructive sample was taken on September 9, 2013, in Trial 1 and on September 16, 2014, in Trial 2 to assess the effects of the treatments on *E. crassipes* by selecting five plants without bias from each mesocosm and capturing the following data: total number of leaves, number of insect-damaged leaves per plant, percent defoliation per plant, the number of biological control agents present, and fresh weight (FW) biomass. Plants were then broken apart, bulked by mesocosm, and placed in Berlese funnels for 7 d to force out and tally internal-feeding insects.

Mesocosms were sampled again as above at harvest, after which all plants were removed and weighed to obtain FW biomass, and a subsample of five plants was dried at 60 C to a constant weight to estimate percent moisture, which was then used to convert FW biomass production per mesocosm to dry weight (DW) biomass. The tanks were drained, and the litterfall at the bottom was collected, weighed, and dried as described earlier to determine DW biomass of litterfall. Mean relative growth rate (MRGR; g DW biomass d^{-1}) was calculated for *E. crassipes* biomass using Equation 1:

$$\text{MRGR} = (\ln\ W2 - \ln\ W1) \,/\, (t_2 - t_1) \qquad [1]$$

where W_1 and W_2 are the DW biomass at the beginning (using the estimate of 96% moisture for FW biomass) (t_1) and end (t_2) of the sampling period, and ln is the natural logarithm. Most of the metrics of interest were affected by the trial, so data were analyzed separately with a two-way ANOVA, and means were separated using LSD with SAS software (v. 9.2, SAS Institute, Cary, NC).

A logistic growth model was parameterized using the variable means averaged over both trials to compare the individual and additive impacts of the insects and the herbicide on the overall growth and posttreatment regrowth of *E. crassipes*. This was done despite the previously mentioned differences in methods design that may have affected the variables. Despite these differences, the general trends were similar in the responses of the variables to the treatments and combining them in this instance likely produced a more conservative set of data for the model.

$$\frac{dP}{dt} = \frac{K}{1 + e^{a - rt}} \qquad [2]$$

where P is population size in terms of grams of DW biomass per square meter; r is mean relative growth rate per week; K is the growth limit value of the population (set at 2,300 g DW biomass m^{-2} as per Reddy and DeBusk [1984]); t is time in weeks; and $a = \frac{K - P_0}{P_0}$, where P_0 is the initial population (36.7 g DW biomass m^{-2}).

The minimum threshold for re-treatment was set at 1,332.2 g DW biomass m^{-2}, which would be roughly equivalent to the mean density of 36.3 plants m^{-2} reported by Center et al. (1999) in herbicide-managed sites in Florida, given the mean (+ SE) DW biomass of *E. crassipes* plants of 36.7 + 1.3 g found in this experiment. In this model, herbicide applications were assumed to have eliminated all but 1 plant within 7 d, and the subsequent population regrowth was based on vegetative propagation, not sexual reproduction or immigration.

Results and Discussion

The insecticides were effective in eliminating or reducing the biological control agents from the plants; sampling found few *N. eichhorniae* adults or larvae and no *M. scutellaris* on sprayed plants (Table 1). The influence of the biological control agents and 2,4-D on some plant parameters varied between the trials, most likely because of differences in the amount of diluent used or the numbers of insects released (Tables 1 and 2). In Trial 1, plant biomass was influenced primarily by the herbicide and secondarily by the biological control agents (Tables 1 and 2). There was a biological control by herbicide interaction that was caused by a change in rank whereby the herbicide reduced plant biomass more when the biological control agents were present (Tables 1 and 2). This pattern was reversed in Trial 2, in which the influence of biological control on plant biomass exceeded that of the herbicide treatments. The interaction between these factors in Trial 2 resulted from the same change of rank as in Trial 1, whereby the influence of the herbicide on biomass was greater in the presence of the biological control agents (Tables 1 and 2). Percent plant defoliation, the percentage of damaged leaves per plant, MRGR, and the number of inflorescences were influenced entirely by the biological control agents in both trials, except for MRGR, which was slightly influenced by the herbicide alone in Trial 2 and through interactions between both main factors in both trials (Tables 1 and 2). These interactions mirrored those of plant biomass with biological control and herbicides. Neither herbicides nor biological control influenced the amount of litterfall from the plant populations in either trial (Tables 1 and 2). Litterfall from mats of *E. crassipes* can promote increases in microbial production with concomitant increases in respiration rates that deplete dissolved oxygen in the water column, which ultimately can harm aquatic fauna (Hall and Meyer 1998; Jansson et al. 2000).

In this study, regrowth of populations of *E. crassipes* was slowed by attack from the biological control agents, which delayed the plant population from reaching its carrying

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Table 1. Final means (±SE) for plant and insect variables from *E. crassipes* experiment with biological control agents and herbicides.[a]

Trial	Insect treatment	Herbicide	Biomass[1]	MRGR[b]	Inflorescences	Litterfall	*N. eichhorniae*[c]	*M. scutellaris*
		kg ha^{-1}	g DW tank^{-1}		no. tank^{-1}	kg DW tank^{-1}	no. plant^{-1}	
1	Control	0	1,784.6 ± 45.3 a	0.008 ± 0.0001 b	138.0 ± 22.4 a	12.6 ± 1.2 a	0.0 ± 0.0 b	0.0 ± 0.0 b
1	Control	2.1	1,113.5 ± 82.5 b	0.017 ± 0.0005 a	147.8 ± 13.5 a	21.7 ± 6.5 a	0.02 ± 0.02 b	0.0 ± 0.0 b
1	Control	4.2	1,051.9 ± 41.4 b	0.016 ± 0.0006 a	143.2 ± 20.4 a	16.6 ± 4.6 a	0.0 ± 0.0 b	0.0 ± 0.0 b
1	Release	0	1,874.8 ± 130.4 a	0.008 ± 0.0003 b	62.0 ± 11.6 b	18.5 ± 4.3 a	3.0 ± 0.6 a	1.4 ± 1.1 a
1	Release	2.1	92.5 ± 63.8 c	−0.001 ± 0.003 c	76.4 ± 13.1 b	25.3 ± 5.3 a	3.4 ± 0.6 a	0.3 ± 0.1 ab
1	Release	4.2	0.9 ± 0.9 c	−0.004 ± 0.004 c	80.0 ± 11.5 b	27.1 ± 4.8 a	0.9 ± 0.2 b	0.4 ± 0.2 ab
2	Control	0	1,276.9 ± 101.03 a	0.007 ± 0.0002 b	334.2 ± 15.1 a	2.2 ± 0.6 a	0.1 ± 0.03 b	0.0 ± 0.0 b
2	Control	2.1	1,218.5 ± 152.9 a	0.015 ± 0.001 a	336.6 ± 12.4 a	2.2 ± 0.3 a	0.04 ± 0.01 b	0.01 ± 0.01 b
2	Control	4.2	728.7 ± 188.8 b	0.010 ± 0.004 ab	338.4 ± 8.3 a	2.3 ± 0.2 a	0.0 ± 0.0 b	0.0 ± 0.0 b
2	Release	0	705.3 ± 67.6 b	0.004 ± 0.0003 bc	170.0 ± 13.6 b	3.6 ± 0.8 a	9.2 ± 1.3 a	4.8 ± 1.5 a
2	Release	2.1	19.4 ± 12.8 c	−0.002 ± 0.001 d	147.0 ± 13.6 b	1.9 ± 0.6 a	4.3 ± 1.1 a	0.4 ± 0.1 b
2	Release	4.2	0.0 ± 0.0 c	0.0 ± 0.0 cd	152.2 ± 9.7 b	2.1 ± 0.1 a	2.4 ± 0.7 b	0.08 ± 0.08 b

[a] Means in a column within trials followed by different letters are significantly different at $P < 0.05$.

[b] MRGR is the mean relative growth rate calculated using this formula: MRGR = $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_1 and W_2 are the DW biomass at the beginning (t_1) and end (t_2) of the sampling period.

[c] *N. eichhorniae* measurements includes both larvae and adults.

capacity by an extra 4 wk (week 30 vs. week 34) (Figure 1). The re-treatment threshold was reached after 9 wk with the reduced rate of herbicide alone (Figure 2A) compared with 11 wk for the operational rate of herbicide alone (Figure 2B). Adding the biological control insects to the reduced rate of herbicide extended the posttreatment interval to 22 wk, an increase of 244%, which ultimately translated into three fewer sprays over the course of a year (Figure 2A). Increasing the rate of herbicide with biological control extended the posttreatment interval by only 2 wk compared with the reduced rate, indicating that the reduced rate of 2,4-D was adequate for control (Figure 2B). Although temperature was not considered in this model, the mean daily temperature from November through February was 24.2 C and 23.1 C in

Table 2. Results of ANOVA for *E. crassipes* parameters with biological control and herbicides as main factors.[a]

Variable	Trial	Biocontrol (B)		Herbicide (H)		B × H	
		df	TSS	df	TSS	df	TSS
			%		%		%
Plant biomass (g DW tank^{-1})	1	1	19.5**	2	31.9**	2	6.3**
Plant defoliation (%)	1	1	27.0**	2	3.6	2	3.4
Damaged leaves (%)	1	1	82.1**	2	1.1	2	1.1
MRGR (g DW biomass d^{-1})	1	1	46.3**	2	1.5	2	25.1**
Inflorescences (no. tank^{-1})	1	1	53.4**	2	1.3	2	0.3
Litterfall (kg DW tank^{-1})	1	1	9.5	2	10.2	2	1.7
Plant biomass (g DW tank^{-1})	2	1	36.5**	2	9.5**	2	8.4**
Plant defoliation (%)	2	1	44.1**	2	2.5	2	2.8
Damaged leaves (%)	2	1	54.6**	2	6.7	2	1.4
MRGR (g DW biomass d^{-1})	2	1	30.3**	2	0.6*	2	8.2*
Inflorescences (no. tank^{-1})	2	1	82.2**	2	0.07	2	0.22
Litterfall (kg DW tank^{-1})	2	1	3.1	2	9.3	2	7.4

[a] Presented are the degrees of freedom (df) and the rounded percentage of variance explained by a factor (TSS) calculated using the formula: TSS = 100 × (factor SS/total SS). SS is the sums of squares.

* $P < 0.05$.

** $P < 0.01$.

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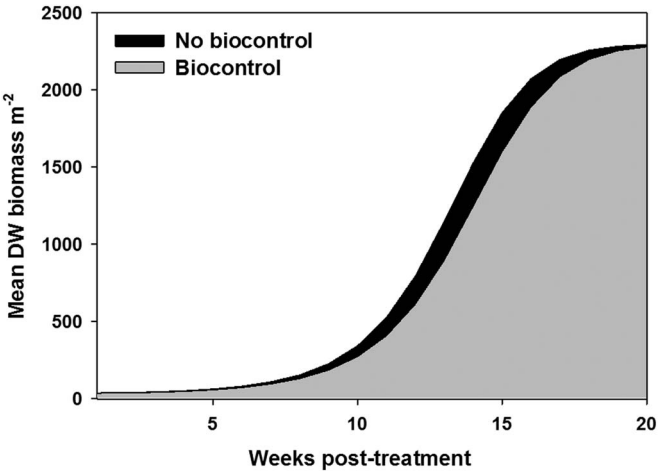

Figure 1. Estimated DW biomass production of *E. crassipes* over time with and without herbivory by two biological control species according to the logistic model $\frac{dP}{dt} = \frac{K}{1+e^{a-rt}}$ (Equation 2).

Ft. Lauderdale during Trials 1 and 2, respectively. Imaoka and Teranishi (1988) estimated that the growth rate of *E. crassipes* increases exponentially with ambient temperatures in the range of 14 to 29 C. Although not a factor at this location, *E. crassipes* growing at sites farther north would likely see longer intervals between herbicide re-treatments because of lower growth rates during the winter months (Reddy and DeBusk 1984; Tucker and DeBusk 1983).

The relatively low densities achieved by *M. scutellaris* in these studies were noteworthy and suggest that most of the reductions in plant parameters were attributed to *N. eichhorniae* (Table 1). This result identified gaps in our current understanding of the dispersal behavior of *M. scutellaris* in mats of *E. crassipes*; the resolution of these questions may guide decisions on how best to deploy them in the field. For example, should deployment be through placement of egg-laden plants within mats, direct release on plants, or some combination thereof?

Another noteworthy event occurred postspray in Trial 1 with the combined reduced rate of herbicide and biological control treatment. Here the insects became highly concentrated on the few surviving plants that were skipped or regrew more quickly than others, apparently by dispersing from the sprayed and now dead and dying plants in the mesocosm. As a result, these plants suffered disproportionate levels of defoliation and herbivory. In previous studies seeking to combine biological control with herbicidal control, spraying patterns were employed that left unsprayed plants in one discrete area or a series of progressively smaller but discrete areas of the plant population as a refuge for the insects (Haag et al. 1988; Haag and Habeck 1991). The outcome in Trial 1 might suggest a different approach of creating refuges within the sprayed mat via intentional skips so that insects like *N. eichhorniae* adults would travel shorter

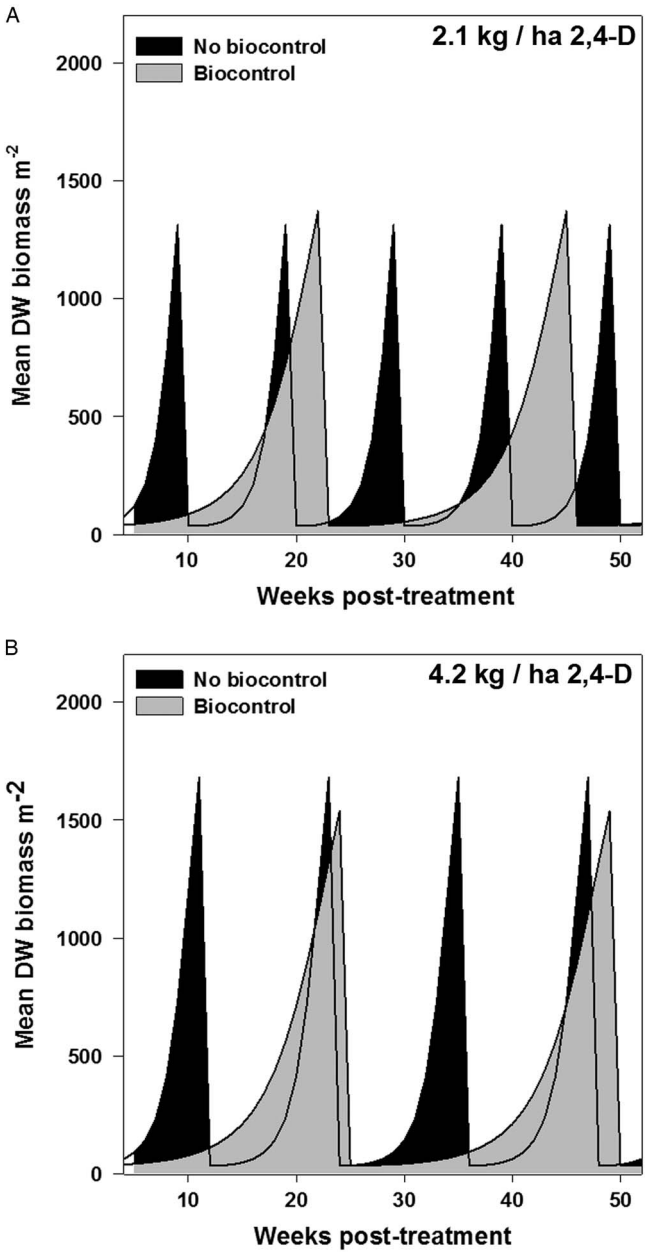

Figure 2. Estimated DW biomass production of *E. crassipes* following reduced (A) or higher (B) rates of 2,4-D treatments in the presence and absence of biological control by *N. eichhorniae* and *M. scutellaris* using Equation 2. Modeled re-treatments using 2,4-D were conducted when DW biomass exceeded 2,300 g DW biomass m^{-2}.

distances to find higher-quality or live plants. Whether the increased herbivory from migrating insects can suppress surviving plants sufficiently while preserving a critical population density of the insects remains to be tested.

Overall, the results were stark for both trials; herbivory by biological control agents significantly boosted the overall

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effectiveness of the herbicide. Averaged over the two trials, the presence of biological control agents more than quadrupled the impact of the reduced rate of 2,4-D and more than doubled the impact of the operational rate of 2,4-D on *E. crassipes* biomass. Similar synergies were reported by Van (1988) when combining the use of *N. eichhorniae* and a plant growth retardant. The cost savings for newer, more expensive herbicides could be considerable if the same pattern holds. Identifying the rate of herbicide that maximizes the impact of both tactics without sacrificing overall efficacy awaits further study. Developing and promoting more balanced maintenance programs may help to maintain public support for the continued funding of important herbicide programs designed to keep waterways and drainages free of invasive plants like *E. crassipes*.

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