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Does water hyacinth (*Eichhornia crassipes*) compensate for simulated defoliation? Implications for effective biocontrol

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ABSTRACT

Biocontrol agents of water hyacinth (*Eichhornia crassipes*), one of the most ubiquitous invasive aquatic species in the world, were introduced in the waterways of Florida, USA, more than 30 years ago but have not been as successful as expected. The high nutrient, high light, warm year-round temperatures and lack of natural predators provide an optimal growth environment for the plant. The current study was designed to test if a compensatory response by the water hyacinth plants to low levels of biomass removal was one of the reasons for the ineffectiveness of biocontrol agents in the successful control of water hyacinth. The plants were exposed to two levels of nutrient (high and low) and three levels (0%, 10% and 80%) of simulated herbivory treatment. The effect of the nutrient and repeated (i.e., chronic) defoliation treatments was determined after 6 weeks. Plants with 10% defoliation did not show any significant difference from control plants in biomass allocation or relative growth rate (RGR) in either nutrient concentration, while 80% defoliation caused a significant decrease in the final RGR under high and low nutrient treatments. High nutrient treatment resulted in higher RGR and allocation to asexual reproduction resulting in higher biomass accumulation compared to the low nutrient treatment, which had higher root growth and allocation to sexual reproduction. Results from this study indicate that water hyacinth can fully compensate for low levels of continuous defoliation regardless of the nutrient concentration, which has implications and important considerations for biocontrol strategies.

1. Introduction

Water hyacinth (*Eichhornia crassipes* [Mart.] Solms) is one of the most productive plants on earth and considered as one of the world's worst invasive aquatic plants (Gopal, 1984; Malik, 2006; Wolverton and McDonald, 1978). Under optimal growing conditions, with high light, temperature and nutrients, the plants can double their numbers every 2 weeks by means of off-shoots. A review by Gopal (1987) reported that the doubling times for water hyacinth varied from 6 to 28 days for weight and from 4 to 58 days for numbers of plants as measured in the open (outside ponds) or in the field. The very fast vegetative reproduction cycle and high mobility of water hyacinth favors its propagation in regions with a tropical climate (Gopal, 1987).

Water hyacinth has received considerable attention for the discovery of potentially effective biocontrol agents. Six natural enemy species of water hyacinth have been released around the world between 1972 and 1996, including: two weevils, *Neochetina bruchi* (Hustache) and *N. eichhorniae* (Warner); two moths, *Niphograpta albiguttalis* (Warren) and *Xubida infusellus* (Walker); a mite *Orthogalumna terebrantis* (Wallwork); and a sap-sucking bug *Eccritotarsus catarinensis* (Carvalho) (see Julien et al., 2001). The primary biocontrol agents presently used against water hyacinth are the *Neochetina* weevils (Julien, 2001).

In the subtropical environment of southern Florida, USA, where water hyacinth is one of the most detrimental invasive aquatic plant species, the long established biocontrol agents (i.e., *Neochetina* weevils) are largely ineffective in controlling the spread of water hyacinth (Center et al., 1999). The waterways where water hyacinth is largely found in Florida are eutrophic and so, given the climate and high nutrient status, the weevils should show a greater impact on water hyacinth growth, especially in the case of *N. bruchi*, as this weevil has been found to be more successful under high nutrient concentrations (Heard and Winterton, 2000). Center et al. (1999) have suggested that the ubiquitous application of herbicides may lead to a continuous lag phase for population growth of biocontrol agents as compared to the water hyacinth plants which have been hypothesized to readily reestablish from abundant seed sources after herbicide treatment. Alternatively, and perhaps facilitated by herbicide application, the ineffectiveness of *Neochetina* weevils controlling the spread of water hyacinth (Center et al., 1999) may be due to the combination of eutrophic

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environment and high light conditions of the South Florida waterways that allow the water hyacinth plants to maintain productivity above the level of weevil herbivory. Furthermore, if a low level of herbivory is present, it may result in an overcompensatory growth response by the water hyacinth plants.

It has been hypothesized that some plants may overcompensate for low levels of herbivory (McNaughton, 1983, 1986; Paige and Whitham, 1987) although the overcompensation hypothesis remains controversial (*e.g.* Belsky, 1986; Belsky et al., 1993; Wise and Abrahamson, 2007). The compensatory continuum hypothesis (CCH) proposed by Maschinski and Whitham (1989) predicts that depending on their access to needed resources as influenced by soil nutrients, water, or interspecific competition, plants may exhibit a negative, neutral, or overcompensatory response to herbivores. The ability of plants to compensate for damage should be highest when they grow in competition-free environments characterized by optimum availability of light, nutrients, and water (i.e., high-resource, low-stress environment); the conditions typically prevalent in the waterways of Florida.

The main focus of this study was to investigate whether the high amount of nutrient availability, as found in the canals of southern Florida, is facilitating the plants to either compensate or overcompensate in growth to a low level of chronic simulated herbivory. We hypothesized that: (1) under high nutrient conditions water hyacinth would overcompensate for low levels (i.e., 10%) of continuous simulated herbivory; (2) under low nutrient conditions compensation for low defoliation would be muted but sufficient to result in no difference in growth between the defoliated and control plants; and (3) that high defoliation (80%) would be too great for compensation to occur regardless of nutrient level and thereby result in the lowest overall growth rates. Our definition of compensation and overcompensation is similar to that of Strauss and Agrawal (1999). If the growth of the defoliated plant is similar to that of the control plant we consider it as compensation while if the growth of the defoliated plants is higher than the control plants it would be considered overcompensation.

Outcomes from the current study will contribute to the understanding of the growth and biomass allocation response of water hyacinth under varying nutrient concentrations and defoliation levels. The findings may provide possible insights as to why the biocontrol of water hyacinth has not been as successful as expected in Florida. They may also assist in providing a greater understanding of the effects on plant growth of defoliation by a potential biological control agent before it is released, which is a neglected aspect of biological control (see Briese, 2004).

2. Materials and methods

2.1. Plant source

Water hyacinth plants used in this study were collected from the canals of the Big Cypress Seminole Indian Reservation in Hendry County, Florida. The plants were cleaned and treated with systemic pesticide and fungicide and grown for 1 month in mesocosms outside the greenhouse facility of Florida Atlantic University, Davie, Florida to facilitate production of similar aged daughter plants that were free from weevils.

At the onset of the experiments 20 water hyacinth daughter plants were selected randomly and harvested destructively to determine the relationship between wet mass and dry mass. The plants were separated into leaves, petioles, stolons and roots and then dried at 70 °C to constant mass. Total plant mass was obtained after weighing all the plant parts. Thus an allometric relationship (dry weight (g) = 0.0354 + 0.0567 wet weight (g), $R^2 = 0.92$) was determined between the wet mass and dry mass. This allometric relationship was used to estimate initial dry mass, which was then used to calculate the relative growth rate at the end of the experiment.

2.2. Experimental design

Nutrient treatments were randomly assigned to 12 equal-sized, round mesocosms (158×53 cm) outside the greenhouse facility. Six mesocosms out of 12 received high nutrient concentrations while the remaining six received low nutrients. Nitrogen and phosphorus were added as potassium nitrate (KNO_3) and potassium dihydrogen orthophosphate (KH_2PO_4), respectively, at concentrations of 50.5 mg N L^{-1} with 2.56 mg P L^{-1} (high) and 5.5 mg N L^{-1} with 0.2 mg P L^{-1} (low). The high nutrient treatment matched the concentration of N and P at which maximum N storage occurs in water hyacinth (Coetzee et al., 2007). The low nutrient concentration was equivalent to the oligotrophic concentration used by Coetzee et al. (2007) and Reddy et al. (1989). Iron chelate (13% Fe) was also added to both high and low concentration treatments at a concentration of 11.2 mg Fe L^{-1} of water.

Eighteen daughter plants were placed in each of the 12 mesocosms. These plants were allowed to equilibrate to the nutrient concentration for 2 weeks before the simulated herbivory treatments were begun. The wet mass of each experimental plant was then recorded and initial dry mass was calculated.

The leaf area of each plant was estimated by measuring the length of the leaf from the petiole to the blade tip and assuming the leaves to be circular. Based on these measurements the leaves of the plants were categorized into large, medium, and small. The numbers of holes to be punched to simulate three levels of insect herbivory were based on the leaf-size categories. To simulate arti-

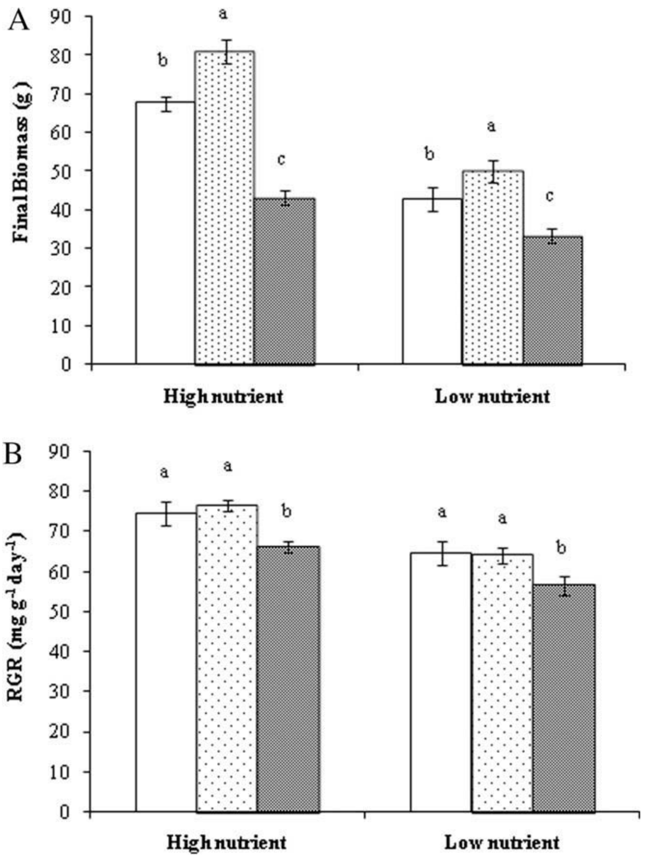

Fig. 1. Mean (±SE) final biomass (A) and final relative growth rate (RGR) (B), under high and low nutrient concentrations and three simulated herbivory treatments, where (□) = 0%, (▒) = 10%, and (▩) = 80% defoliation, respectively. Different letters within a nutrient treatment are significantly different at $P < 0.05$.