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RESEARCH ARTICLE

Feeding impact of the planthopper *Taosa longula* (Hemiptera: Dictyopharidae) on water hyacinth, *Eichhornia crassipes* (Pontederiaceae)

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Taosa longula Remes Lenicov (Hemiptera: Dictyopharidae), a planthopper native to South America, is a candidate for the biological control of water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae), a serious weed worldwide. Biological control requires agents that are not only specific but also effective. Damage caused by sap-sucking insects is difficult to assess. In this work we designed an experimental and analytical procedure to evaluate the potential damage of *T. longula* on water hyacinth. The damage that *T. longula* causes to the clonal reproduction, biomass production, and growth of water hyacinth was studied through a paired greenhouse trial with floating cages. The performance of the plant, starting from two plants per treatment, was evaluated at different insect densities (5, 10, 15 and 20 nymphs per cage) until all the nymphs moulted to adults. The tests showed that individual growth and biomass production of water hyacinth was reduced due to the effect of the insect feeding above five nymphs per cage. The number of new plants produced by clonal reproduction was only significantly different above 15 nymphs per cage. These results suggest that this planthopper could be an effective agent for the biological control of water hyacinth.

Keywords: water hyacinth biocontrol; hemipteran feeding damage; paired feeding tests

Introduction

Water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae), is a South American aquatic weed distributed worldwide. Several characteristics make it one of the most aggressive and problematic weeds in the world (Holm, Plucknett, Pancho, and Herberger 1977), such as its ability to resprout from the rhizome, copious seed production, propensity for rapid branching and vegetative reproduction and high canopy. These traits allow it to quickly dominate the area and compete for light, thereby ensuring rapid invasion and reinvasion of water bodies, precluding potential competition (Center and Spencer 1981).

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Different control strategies have been used to mitigate the adverse effects of this weed, but biological control is thus far the only method that has provided environmentally friendly, cost-effective and long-term control (Harley 1993; Harley, Julien, and Wright 1996; Julien et al. 1996). Yet, even though nine biological control agents for water hyacinth have been released in many countries (Reeves and Lorch 2012), the problems caused by this weed worldwide are not totally solved (Center, Hill, Cordo, and Julien 2002; Sosa, Cordo, and Sacco 2007). Factors that limit the effectiveness of biocontrol include herbicidal or mechanical control measures interfering with agent development, shallow water preventing damaged plants from sinking, ephemeral water bodies, toxicity effects in polluted waters and small releases, as opposed to mass or serial releases (Hill and Olckers 2001). More mobile agents, with shorter life cycles and high reproductive capacities, may survive non-cyclical disruptions, such as those induced by herbicide applications and mechanical harvesting (Center, Dray, Jubinsky, and Grodowitz 1999). Three agents that may exhibit these characteristics have been recently evaluated, *Megamelus scutellaris* Berg (Hemiptera: Delphacidae), *Thrypticus truncatus* Bickel and Hernández (Diptera: Dolichopodidae) and *Taosa longula* Remes Lenicov (Hemiptera: Dictyopharidae) (Hernández 2008; Hernández, Brentassi, Sosa, Sacco, and Elsesser 2011a; Tipping, Center, Sosa, and Dray 2011).

All of the agents released are chewing species except for two: *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) (Coetzee, Center, Byrne, and Hill 2005), which is a cell content feeder, and *M. scutellaris* (Tipping et al. 2011), which is a sap feeder (Hernández et al. 2011a). Sap feeders remove assimilates from phloem and xylem or from individual cells of their host plants, resulting in reduced growth, reproduction and photosynthesis (Zvereva, Lanta, and Kozlov 2010). Plant responses to hemipteran herbivory comprise both constitutive and induced mechanisms of defence, and both are costly for the plant, forcing it to allocate resources to the production of protein and secondary defence metabolites. The plant defence cost together with the direct loss of large proportions of the primary plant production may result in lower fitness (Kaloshian and Walling 2005).

T. longula is a planthopper of neotropical distribution from northern Argentina to Peru. It exists throughout the native tropical distribution of water hyacinth, and does not establish in the more temperate parts of the plant's distribution (Hernández, Sacco, and Cabrera Walsh 2011b). The life cycle of *T. longula* is closely associated with water hyacinth and its micro-environment. The females oviposit on average 70 eggs per clutch, inserting them in the petioles of water hyacinth. The young nymphs typically feed in groups on the underside of the leaf laminae. The late instars became more solitary, and the adults are mostly found individually in the upper canopy (Remes Lenicov and Hernández 2010). Laboratory tests indicate *T. longula* is highly specific to water hyacinth. Furthermore, it could in principle coexist with minimum interference with the other recently released sap-feeding species, *M. scutellaris*, given marked differences in their feeding sites (Hernández et al. 2011a,b).

In addition to the loss of metabolites caused by direct feeding, the planthopper *T. longula*, a sap feeder, produces salivary sheaths to reach the vascular tissues. These stylet pathways in turn cause blockages of the vascular tissues with salivary deposits, promoting cellular alteration or death (Spiller, Koenders, and Tjallingii 1990; Will and van Bel 2006; Hernández et al. 2011a).

We assess the negative impact of different densities of *T. longula* nymphs on water hyacinth fitness expressed as clonal reproduction, biomass production and canopy development, under controlled laboratory conditions, in order to satisfy the requirements of releasing a host-specific, damaging agent.

Materials and methods

Experimental design

Studies were conducted at the Fundación para el Estudio de Especies Invasivas (FUEDEI) (Formerly USDA-ARS-South American Biological Control Laboratory, SABCL) between 2006 and 2007. Cultures of *T. longula* were established at the laboratory from eggs collected on water hyacinth plants in Herradura (S26°29′28″; W58°18′37″), Formosa Province, Argentina. Water hyacinth petioles with *T. longula* oviposition scars collected in the field were incubated in the laboratory, in groups of 10–20 petioles in 40 × 27 × 8-cm plastic trays lined with moist tissue paper, and covered with adhesive film. The trays were periodically checked for newly emerged nymphs to be used in the tests. First instars were collected with aspirators and placed directly on the test plants.

The experiment was conducted in 160 × 100 × 35-cm canvas pools (ca. 350 litres), in a 6 × 4 m greenhouse. Two floating cages were placed in each pool, which had 5 cm of loamy soil in the bottom and was filled with water fertilised with full-strength Sato and Kondo (1981) solution, so as to provide optimal nutritional conditions for the test plants. Each cage consisted of a 60 × 80-cm floating frame made with 5-cm diameter PVC pipes, to which a 70-cm high wire dome was attached. A polyester fabric hood (white, 0.354 mm mesh size) was draped over the wire dome, with the hem submerged in the water to prevent escapes. Each hood had a 60-cm zipper at one end to allow access to the plants. Two water hyacinth plants of similar size and equal number of leaves were assigned at random to each cage, which had enough open space left over to allow substantial plant growth. The plants came from a laboratory cohort grown from field plants from which the first spring clones had been separated and grown in a different pool. Every time the cohort sprouted new clones, these were separated, and a new cohort was formed to be ready for the experiments. This way it was possible to initiate every experiment with plants of similar size and equal number of leaves. The original stock of the experimental plants was from Herradura. The mean dry weight of a random sample of five similar plants was taken at the onset of every trial, to provide an initial estimate of biomass for comparison with the final biomass resulting from the tests. Nymphs of *T. longula* were placed on the plants in one of the cages, while the plants of the twin cage remained as controls. Each trial consisted of four different insect densities, 5, 10, 15 and 20 nymphs per cage, and was replicated five times (i.e. five pools per treatment). The result was a paired design wherein water and light conditions were identical in test and control treatment cages. Each cage was monitored until all surviving *T. longula* nymphs had moulted to adults.

Three plant growth parameters were evaluated: plant biomass, clonal reproduction and canopy height. Cages remained undisturbed during the first two weeks to allow the insects to settle. Two weeks into the experiment, the height of the canopy, calculated as the mean of the five highest leaves from the water surface to the tip of

the leaf, began to be recorded every week. At the end of the experiment, when the last nymphs moulted to adults, the canopy was measured for the last time, and the total number of plants per cage was counted, as a measure of the clonal reproduction of the plant. Lastly, all plants from each cage were placed in paper bags and dried in an oven at 60°C until constant weight.

Due to greenhouse space limitations, the trials could not be carried out simultaneously (15 nymphs, 1–26 December 2006; 5 nymphs, 26 December 2006–21 January 2007; 20 nymphs, 22 January–23 February 2007; 10 nymphs, 20 March–22 April 2007), so they developed during periods with varying weather conditions. This was expected to result in different growth responses, even among the controls of the different trials. Photoperiod and temperature data for the experimental periods were obtained from a weather station located 20 km west of the laboratory.

Data analyses

The inability to test all insect densities simultaneously imposed some limitations on analysis. Dry biomass and final number of plants per pool were tested for normality with Shapiro–Wilk tests, and compared within trials with Student's *t*-tests. The canopy growth curves were compared within trials with Wilcoxon's Signed Ranks tests (SYSTAT 2004).

An alternative was examined to standardise the different trials and achieve some level of comparability between them. It was hypothesised that the differences in the slopes of the canopy growth curves between controls and treated cages within trials could be a fair measure of the growth divergence between them. A growth divergence index was calculated based on standardised angle differences that could then be compared among treatments. Under this hypothesis, the angles separating the growth curves of controls and treated cages were taken to describe damage levels. This supposition was based on the principle that the experimental design guaranteed that any difference between the growth curves of treated plants and their respective controls was owed exclusively to the effect of herbivory. So canopy growth data for each individual pool were tested for normality, and a least squares linear regression (canopy growth on days) was adjusted to the data of each cage. Through this procedure every growth curve was transformed to its most significant straight line. This provided a matrix of 40 regression equations, 5 for each treatment and their controls. The slopes (m) of these regressions were then transformed to angles ($\theta = \tan{-1}\ m$). Finally, a new matrix of damage indices was obtained by calculating the moduli of the differences in rise between each repetition and its control ($\Delta\theta = |\theta$ control $- \theta$ treated$|$), consisting of five cases (each pool) per four treatments (number of nymphs). The treatments were analysed with an ANOVA followed by Bonferroni's unplanned comparisons (SYSTAT 2004).

Results

Initial results

T. longula feeding affected plant growth dramatically in some cages. The symptoms observed were a general yellowing of the leaf laminae, stunted development and premature senescence of leaves (Figure 1).

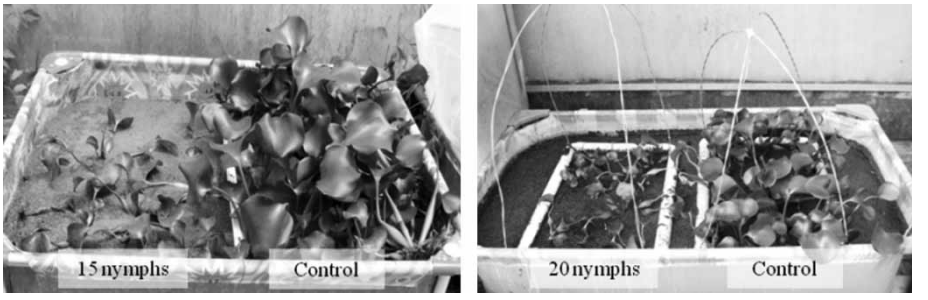

Figure 1. Feeding effect of *T. longula* on water hyacinth at the end of trial: left of each pool, treated plants; right, controls. Right photograph: note design of the floating cages without the fabric hoods.

The mean number of clones was consistently lower in the treatment than the control cages (Table 1), but the difference was significant only for the 20 nymphs treatment ($t = 3.36$, $P = 0.01$). In the other treatments it varied widely among pools, even within trials, finding in some cases more plants in the treatment than the control cages.

The average dry weight of a random sample of plants at the onset of the experiments was 19 ± 0.6 g (mean $\pm$ SE). The biomass difference was significant in all except the five nymphs treatment ($t = 3.69$, $P = 0.013$; $t = 2.48$, $P = 0.038$; $t = 3.74$, $P = 0.006$, for the 10-, 15- and 20-nymph treatments, respectively). The greatest differences in absolute terms within trials were observed in the 15-nymph trials, followed by the 20-, 10- and 5-nymph trials (Table 2). However, total plant biomass with 5 nymphs was 94% of the control, 10 nymphs: 42%, 15 nymphs: 44% and 20 nymphs: 56%. Plant biomass increased greatly during the course of every trial, except in the 10-nymph trials, which took place during early autumn, instead of summer like the other experiments (Table 2). Temperatures and photoperiod for the 5-, 15- and 20-nymph experiments were very similar, whereas during the 10-nymph trials there were 2–3 hours less daylight, and temperatures were between 3.6 and 6 degrees lower, depending on which average is considered. However, development from first instar to adult took the longest in the 20-nymph trial (Table 3).

Canopy height of the treated plants was significantly affected by *T. longula* feeding in all trials except the 5-nymph trials ($Z = 2.56$, $P = 0.005$; $Z = 4.26$, $P = 0.002$; $Z = 3.7$, $P < 0.001$, for the 10-, 15- and 20-nymph tests, respectively). Yet in every case canopy height showed increasing divergence with time between controls and treated cages. Furthermore, final canopy height was on average lower than initial height in the significant treatments, suggesting feeding produced stunting (Figure 2).

Table 1. Final number of plants per pool and trial.

	Pool#							
	5 nymphs	Control	10 nymphs	Control	15 nymphs	Control	20 nymphs	Control
Sum	47	58	29	39	141	195	61	89
Mean	9.4	11.6	5.8	7.8	28.2	39	12.2	17.8
SE	0.42	0.69	0.79	0.46	0.87	0.76	0.31	0.30

Table 2. Final biomass (g) of water hyacinth plants exposed to different densities of *T. longula*.

	Biomass per trial							
	5 nymphs	Control	10 nymphs	Control	15 nymphs	Control	20 nymphs	Control
Sum	491.5	521.7	36.4	85.9	271	613.6	165.5	294.3
Mean	98.3	104.34	7.28	17.18	54.2	122.72	33.1	58.86
SE	3.02	5.01	0.41	0.89	2.13	4.03	1.30	1.24

Additional analyses

The index formed by the differences among the rise of the regression lines from the canopy growth curves showed a different situation (Table 4). The highest mean differences were observed between the 10-nymph trial and their controls, followed by the 15-, 20- and 5-nymph trials, respectively. The ANOVA was significant ($F = 3.32$, $P = 0.046$), and the highest score was significantly different from the lowest (Figure 3). Given the experimental design, these differences could only respond to the effect of *T. longula* feeding.

Discussion

T. longula feeding produced a clear reduction in canopy development and biomass. From visual observations, *T. longula* feeding resulted in chlorosis, shorter leaves, and generally weakened and stunted plants (Figure 1). These effects are probably attributable to the typical effects of planthopper feeding, which tends to cause fitness reduction through the activation of herbivory resistance mechanisms and consumption of photosynthates (Backus, Serrano, and Ranger 2005; Kaloshian and Walling 2005; Hernández et al. 2011a; Zvereva et al. 2010). Clonal reproduction was also generally lower in the treated cages, but statistically significant differences were observed only in the 20-nymph treatment. Production of clones by water hyacinth in response to feeding stress appears to be affected by a combination of factors. In an experiment manipulating herbivore density and nutrient levels in water hyacinth cultures, damage by *Neochetina* spp. (Coleoptera: Curculionidae) invariably affected clonal growth (Heard and Winterton 2000). However, it must be noted that these herbivores consume meristematic tissues, so the type of damage is not comparable to a sap feeder's. Damage by a true defoliator, *Cornops aquaticum* (Bruner) (Orthoptera:

Table 3. Weather statistics during the experiments, and maximum duration of nymphal stage.

Treatment	Photoperiod[a]	Avge. t°[b]	t° max[c]	t° min[d]	Growth[e]
5 nymphs	14.3 ± 0.05	25.3 ± 1.29	30.0 ± 1.56	21.2 ± 1.29	20 ± 0.98
10 nymphs	11.5 ± 0.11	20.8 ± 0.89	23.9 ± 0.89	17.6 ± 1.34	27 ± 1.03
15 nymphs	14.4 ± 0.03	25.0 ± 0.76	29.5 ± 1.07	21.1 ± 1.34	23 ± 1.43
20 nymphs	13.6 ± 0.0.12	24.2 ± 1.16	29.0 ± 1.52	19.8 ± 1.29	32 ± 1.07

[a]Mean hours of light for the duration of the experiment (± SE).
[b]Mean average temperature for the duration of the experiment (± SE).
[c]Mean maximum average temperature for the duration of the experiment (± SE).
[d]Mean minimum average temperature for the duration of the experiment (± SE).
[e]Mean days from first instar to adult (± SE).

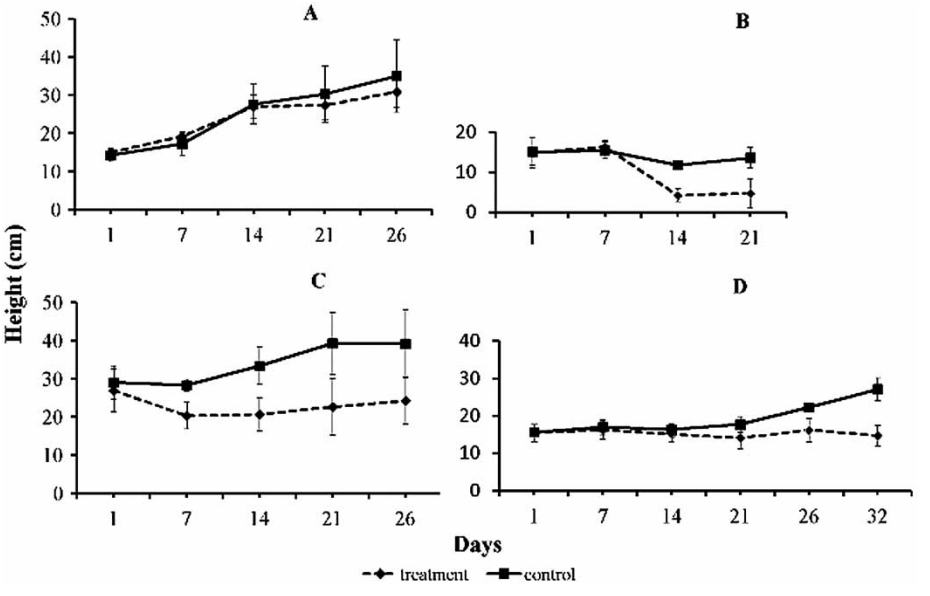

Figure 2. Comparison of the growth of the water hyacinth patch in terms of canopy height for the four *T. longula* nymph densities (mean of five highest leaves ± SD): A, 5 nymphs; B, 10 nymphs; C, 15 nymphs; D, 20 nymphs.

Acrididae), only affected clonal growth at low nutrient levels (Bownes 2008). On the other hand, the cell content feeder *E. catarinensis* affected clonal reproduction significantly over a period of two months (Coetzee, Byrne, and Hill 2007). Regardless, since canopy and biomass differences were significant, it is clear from the results that *T. longula* feeding caused significant, sometimes drastic, growth reductions in water hyacinth, except perhaps for the five nymphs treatment.

The size of the experimental units precluded both the use of a walk in chamber with controlled temperature, and evaluating the four *T. longula* densities simultaneously, because each series of trials took up ca. 30 m^2 of greenhouse space, which was as all that was available. However, smaller units, and/or controlled conditions would have compromised the objective of the test, which was to allow space for the growth of the water hyacinth patches, emulating field conditions. Consequently, growth conditions were not equal for every test because of climatic differences (i.e. the 10-nymph test developed under lower temperatures and shorter

Table 4. Angle differences (in degrees) between the minimum square regression lines of the canopy growth curves for each experimental pair of cages.

Pool #	5 nymphs	10 nymphs	15 nymphs	20 nymphs
1	9.3	16.0	18.6	23.8
2	6.4	18.1	46.2	20.2
3	9.9	36	9.5	23.5
4	21.7	53.1	33.2	15.1
5	11.8	40.4	28.0	19.3

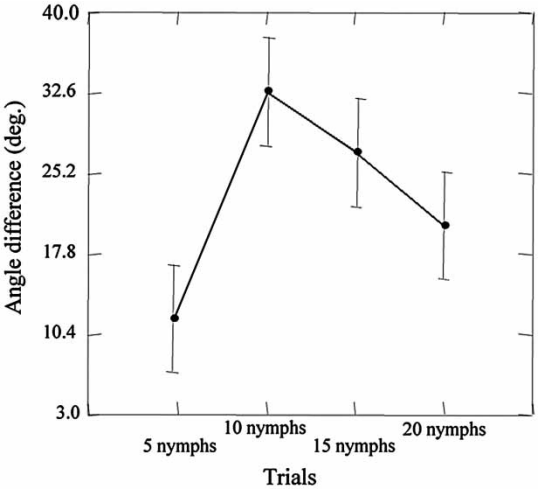

Figure 3. Canopy growth index differences, calculated as mean differences in rise (degrees ± SE) of regression lines on canopy growth curves, for the different densities of *T. longula* on water hyacinth.

photoperiods than the other trials). In any case, we believe we have achieved the objective of isolating the effect of the insect feeding damage quite effectively. If this premise is correct, the divergence between treated and control cages, as expressed by the divergence in the angles of the regression slopes, might let us conclude that the effect of the feeding of *T. longula* was significant above a density of five nymphs. A critical mass of 10 nymphs per cage had a significant effect on plant growth. The higher densities (15 and 20 nymphs) caused a lower divergence between controls and treated cages, suggesting they may have been excessive, and some interspecific competition may have taken place.

We realise this treatment of the data, i.e. comparing non-simultaneous experiments, is highly speculative. Also that the climatic differences probably cannot be ruled out no matter what. Yet, this analysis could also find support in the fact that development took longest at the highest density (Table 3), suggesting intraspecific competition may have affected nymph development. Also, there were lower relative biomass differences at 15 and 20 nymphs per cage, than at 10 nymphs.

A previous publication established the virtually complete specificity of *T. longula* on water hyacinth, and its presence year-round in its native range (Hernández et al. 2011b). The addition of the results of this study indicates that *T. longula* fulfils three important traits for a suitable biological control candidate: feeding and oviposition specificity, early appearance in the field and potentially strong effects on the development of the host plant. We conclude that this species could be a valuable tool to manage the water hyacinth in its exotic range.

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