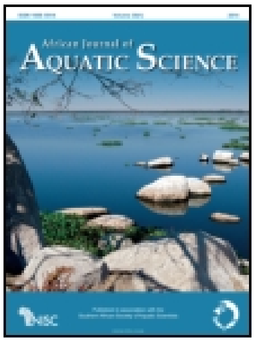

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Effect of water trophic level on the impact of the water hyacinth moth *Niphograpta albiguttalis* on *Eichhornia crassipes*

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Eutrophication contributes to the proliferation of alien invasive weed species such as water hyacinth *Eichhornia crassipes*. Although the South American moth *Niphograpta albiguttalis* was released in South Africa in 1990 as a biological control agent against water hyacinth, no post-release evaluations have yet been conducted here. The impact of *N. albiguttalis* on water hyacinth growth was quantified under low-, medium- and high-nutrient concentrations in a greenhouse experiment. *Niphograpta albiguttalis* was damaging to water hyacinth in all three nutrient treatments, but significant damage in most plant parameters was found only under high-nutrient treatments. However, *E. crassipes* plants grown in high-nutrient water were healthier, and presumably had higher fitness, than plants not exposed to herbivory at lower-nutrient levels. *Niphograpta albiguttalis* is likely to be most damaging to water hyacinth in eutrophic water systems, but the damage will not result in acceptable levels of control because of the plant's high productivity under these conditions. *Niphograpta albiguttalis* is a suitable agent for controlling water hyacinth infestations in eutrophic water systems, but should be used in combination with other biological control agents and included in an integrated management plan also involving herbicidal control and water quality management.

Keywords: biological control, integrated management, nutrient regimes, plant fitness

Introduction

Eutrophication is one of the most serious threats facing South African water bodies as a result of rapid increases in urban and industrial development (du Plessis and van Veelen 1991; Oberholster and Ashton 2008; van Ginkel 2011). Such development increases pollution and effluent discharge, disturbing aquatic ecosystems (du Plessis and van Veelen 1991). Eutrophication of freshwater habitats increases their vulnerability to invasive alien species, such as water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laub. (Pontederiaceae), which thrives under high-nutrient conditions (Reddy et al. 1989; Coetzee and Hill 2012).

Water hyacinth is considered one of the world's most problematic weeds, invading over 50 countries worldwide (Julien et al. 2001). It was introduced into South Africa for its ornamental properties in the early 1900s, and has since spread across the country (Cilliers 1991). With a rapid growth rate and no natural enemies, water hyacinth takes over slow-flowing freshwater bodies causing siltation, increased acidity, deoxygenation and suppression of natural vegetation (Penfound and Earle 1948; Hill 2003).

A biological control programme was initiated against water hyacinth in South Africa in 1974 and, since then, a suite of seven arthropods and one pathogen have been released (Coetzee et al. 2011). Despite this, biological control success has been limited due to a number of factors including climate incompatibility and eutrophic waters (Hill and Olckers 2001). Studies have shown that eutrophication reduces the degree of control by some water hyacinth control agents such as the weevils *Neochetina eichhorniae* Warner and *Neochetina bruchi* Hustache (Coleoptera: Curculionidae) (Heard and Winterton 2000) and the mirid *Eccritotarsus catarinensis* Carvalho (Hemiptera: Miridae) (Coetzee et al. 2007). Increased nutrient availability is an important extrinsic factor in promoting plant tolerance to herbivory, a process known as plant compensation (Maschinski and Whitham 1989; Strauss and Agrawal 1999) whereby plants have the ability to regrow after herbivory by adjusting their resource allocation or physiology (Strauss and Agrawal 1999; Hawkes and Sullivan 2001). The 'continuum of responses' model predicts that the probability of compensation for herbivory increases with increasing resource levels (Maschinski and Whitham 1989). Therefore, to overcome current limitations in biological control agent establishment, it may be more prudent to assess how the target weeds and agents respond to varying nutrient conditions and then to release the agents where they are most suited (McEvoy and Coombs 1999).

This study assessed the ability of the South American moth *Niphograpta albiguttalis* Warren (Lepidoptera: Crambidae) to control water hyacinth infestations that occur in eutrophic water bodies throughout South Africa. *Niphograpta albiguttalis* was discovered in South America in 1968 (Julien et al. 2001) and, after testing, was found to be a suitable biological control agent as it can disperse over long distances (up to 4 km a day), is tolerant of variable climates, has a short generation time (about 35 days from egg to egg), high fecundity (up to 300 eggs per female) and, most importantly, is host-specific to water hyacinth (Cilliers 1991; Julien et al.

2001; May and Coetzee 2013). Adult females oviposit on the leaves of water hyacinth, primarily in areas where the epidermis has been damaged (Hill and Cilliers 1999). Larvae develop through five instars, tunnelling into petioles and feeding below the epidermis, resulting in damage 'windows'; older larvae feed down towards the central rosette (Julien et al. 2001), eventually leading to the plants becoming waterlogged and sinking (Center and Van 1989).

In Africa, *N. albiguttalis* was first released in Zambia in 1971 and was later released in a further 13 countries, becoming established in only six of them (Julien et al. 2001). In South Africa, it was first released in 1990 at only a few locations, and has since established under a wide range of climatic conditions from tropical KwaZulu-Natal to the cold, high-altitude Vaal River catchment (Hill and Cilliers 1999). With a wide range of climatic tolerance and a preference for younger, bulbous-petiole plants, *N. albiguttalis* population sizes can be highly varied (Hill and Cilliers 1999; May and Coetzee 2013). To date, no post-release evaluations have been conducted to determine the degree of control and, furthermore, no mass-rearing programmes have been instituted (Coetzee et al. 2011).

Thus, the objective of the present study was to investigate the impact of *N. albiguttalis* on water hyacinth under different nutrient conditions typical of South African water bodies, in order to understand establishment patterns and to make predictions on where, and to what extent, the moths will be able to control water hyacinth in various water systems in South Africa.

Materials and methods

Study organisms

The study was conducted at Rhodes University, South Africa, where cultures of both water hyacinth and the moth *N. albiguttalis* were established. Water hyacinth plants were collected from stock cultures maintained at the Department of Zoology and Entomology. *Niphograpta albiguttalis* was collected on 10 March 2009 from Bon Accord Dam, Gauteng (25°37'45'' S, 28°11'21.9'' E), an earth-fill dam situated 15 km north of Pretoria at an altitude of 1 205 m. The site has a savanna climate with warm wet summers and mild dry winters with average maximum temperatures reaching 29 °C and a minimum of 3 °C (www.climate-zone.com/climate/south-africa/celsius/pretoria.htm; accessed 15 July 2013).

Water hyacinth plants were grown in four 40 cm × 60 cm plastic tubs filled with 66 litres of borehole water in a greenhouse tunnel, where temperatures ranged from 17 to 23 °C, at three nutrient levels – oligotrophic (low), eutrophic (medium), and hypertrophic (high) – based on nitrogen concentrations established by Reddy et al. (1989) as significant for water hyacinth growth (Table 1). A commercial slow-release fertiliser, Osmocote Exact™, was added to each treatment at low, medium and high concentrations. However, high-nutrient treatments were increased to match the nitrogen and phosphorus concentrations of hypertrophic water bodies in South Africa (DWAF 1996) (Table 1) by adding 0.29 g KNO_3 l^{-1} (= 40 mg N l^{-1}) and 6.82 mg KH_2PO_4 l^{-1} (= 1.55 mg P l^{-1}) to the high-nutrient treatments. Commercial iron chelate (33 mg l^{-1}) was also added to the water to prevent chlorosis of the plants. Three young water hyacinth plants were placed in each tub to allow for a bulbous petiole growth form, because adult female moths prefer to oviposit on this growth form (Julien et al. 2001). The plants were cultivated at the test concentrations for three months before the experiment commenced.

Experimental design

After three months, 20 plants from each stock plant culture grown at the three nutrient levels were placed individually into 10-litre plastic buckets at the same nutrient concentrations in which they were grown. One second instar larva collected from the insect stock culture was placed on each of the 10 test plants, at each nutrient level, while the 10 control plants at each nutrient level received no moth larvae. All the buckets were covered with netted sleeves to prevent emerging adult moths from escaping and to keep growing conditions consistent. Water levels were maintained at 9 litres throughout the experiment.

At the start of the experiment, daughter plants were removed and plant growth parameters of the test plants were measured to ensure that the nutrient treatments had indeed affected the plants. Plant growth parameters included the number of stems, length of the longest stem, and diameter of the widest stem. The experiment was run for 5 weeks to ensure sufficient time for moth pupation, after which no further damage would occur. At the end of the sample period, the plant growth parameters were measured again, as well as individual plant wet weight biomass. Wet weight was measured instead of dry weight because both measures are highly correlated (TD Center, United States Department of Agriculture, Agricultural Research Service, unpublished data), and fresh weight was the more expedient measure (Coetzee et al. 2005). The number of petioles damaged in the herbivory treatment was counted and the proportion of damaged stems calculated as an indication of the extent of larval feeding.

General linear models (GLMs) compared differences in plant parameters at the three nutrient levels between the herbivory treatment and control plants at the beginning and end of the experiment. Fisher's least significance difference (LSD) *post hoc* tests determined any significant differences between the variables. All analyses were conducted in Statistica v11.

Results

After the initial three-month growing period, water hyacinth plants from the three nutrient treatments were significantly different from one another in terms of number of petioles ($F_{2,57}$ = 40.070; p < 0.0001), length of the longest petiole ($F_{2,57}$ = 36.764; p < 0.0001) and petiole diameter ($F_{2,57}$ = 13.481; p < 0.0001). Plants grown at the high-nutrient level were visually darker green in colour, indicating higher chlorophyll levels and therefore higher plant productivity (Yang et al. 2003). Low-nutrient treatment plants were more yellow in colour, indicating the presence of nutrient deficiency, which is associated with reduced photosynthetic activity (Yang et al. 2003).

After the 5-week herbivory experiment, the control plants that were not exposed to *N. albiguttalis* herbivory were significantly different in all measured parameters under

Table 1: Water nutrient concentrations at which water hyacinth plants were grown, and corresponding trophic classification according to South African water quality guidelines (DWAF 1996)

Nutrient concentration	Osmocote Exact™ (g l^{-1}) (= N mg l^{-1}, P mg l^{-1})	KNO_3 (g l^{-1}) (= N mg l^{-1})	KH_2PO_4 (mg l^{-1}) (= P mg l^{-1})	Trophic classification
Low	0.11 (0.5, 0.004)			Oligotrophic
Medium	0.40 (4.5, 0.015)			Eutrophic
High	0.68 (8.5, 0.48)	0.29 (40)	6.82 (1.55)	Hypertrophic

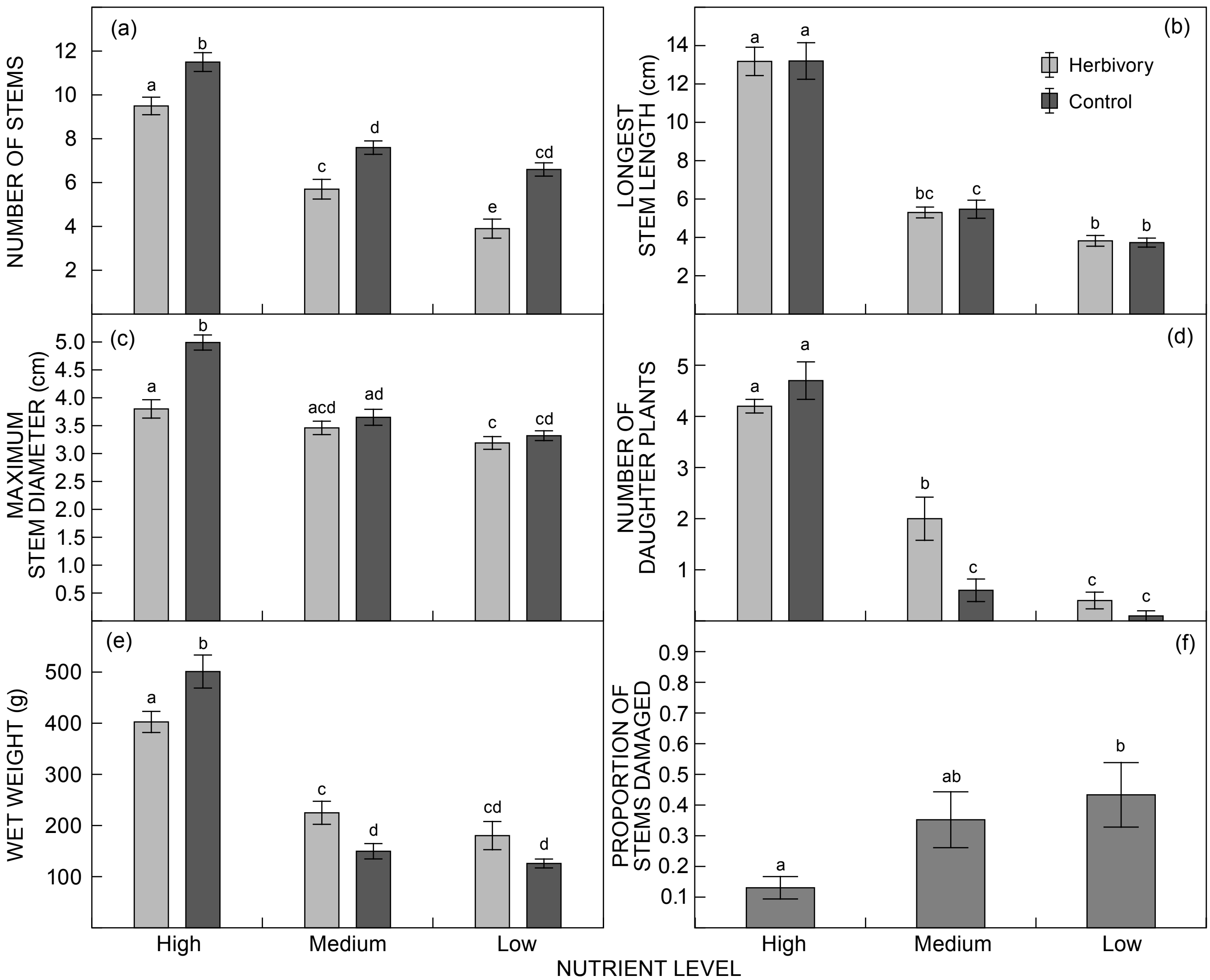

Figure 1: Differences in water hyacinth growth parameters between herbivory treatments at the end of the 5-week experiment under high-, medium- and low-nutrient conditions for (a) number of stems, (b) maximum stem length, (c) maximum stem diameter, (d) number of daughter plants, (e) plant wet weight biomass, and (f) proportion of stems damaged by *Niphograpta albiguttalis* larval feeding. Error bars represent standard error of the mean. Means compared by general linear models (GLMs); different letters above the bars indicate significant differences (Fisher's least significant difference [LSD], $p < 0.05$)

the different nutrient conditions (Figure 1). The number of petioles ($F_{2,54}$ = 192.909, p = 0.0001) (Figure 1a), longest petiole length ($F_{2,54}$ = 259.297, p = 0.0001) (Figure 1b), maximum petiole diameter ($F_{2,54}$ = 85.694, p = 0.0001) (Figure 1c), number of daughter plants produced ($F_{2,54}$ = 45.830, p = 0.0001) (Figure 1d) and total wet weight biomass

($F_{2,54}$ = 175.10, p = 0.0001) (Figure 1e) were all significantly increased under high-nutrient conditions, compared to those in the medium- and low-nutrient treatments. Longest petiole length under the medium-nutrient treatment was significantly longer than under low nutrients (Figure 1b) but, besides this parameter, no other significant differences were found between medium- and low-nutrient controls (Figure 1). Despite the lack of statistical significance, in the absence of herbivory, all plant parameters were smaller on average in low-nutrient treatments than in medium treatments.

The damage inflicted by *N. albiguttalis* resulted in a significant reduction in the number of petioles in all three nutrient treatments ($F_{2,54}$ = 7.746, p = 0.02) (Figure 1a) but did not affect longest petiole length in any of the nutrient treatments ($F_{2,54}$ = 0.060, p = 0.970) (Figure 1b). Maximum petiole diameter was significantly reduced by *N. albiguttalis* feeding at the high-nutrient treatment, where there was a shift from elongate petioles to large bulbous petioles, but had no significant effect at medium or low treatments ($F_{2,54}$ = 10.516, p = 0.0001) (Figure 1c). The number of daughter plants was not affected by herbivory at high- or low-nutrient treatments but, under medium-nutrient conditions, more daughter plants were produced by plants exposed to *N. albiguttalis* compared with control plants ($F_{2,54}$ = 9.203, p = 0.010) (Figure 1d).

The proportion of petioles damaged by *N. albiguttalis* was significantly affected by nutrient treatment (Figure 1f). Under high-nutrient levels, a significantly lower proportion of petioles was damaged than at low nutrients, while the proportion of petioles damaged under medium-nutrient levels was intermediate and not significantly different from either low- or medium-nutrient treatments ($F_{1,27}$ = 2.825, p = 0.077) (Figure 1f). The increase in the proportion of petioles damaged with decreased nutrients was due to the greater petiole lengths of the plants grown under high nutrients (Figure 1b).

Wet weight biomass was significantly reduced by *N. albiguttalis* in high-nutrient treatments, but significantly increased in medium-nutrient treatments ($F_{2,54}$ = 8.899, p = 0.0005) (Figure 1e). Mean wet weight biomass was greater in replicates exposed to herbivory than in controls under low nutrients without herbivory, but this effect was not significant (Figure 1e). The reduction in wet weight biomass under herbivory that was recorded at high-nutrient levels can be attributed to reduced biomass accumulation due to the damage inflicted by *N. albiguttalis*. This is also supported by the decrease in the number of stems as a result of herbivory in the high-nutrient treatment (Figure 1a).

Discussion

Niphograpta albiguttalis negatively impacted water hyacinth under all nutrient conditions, but its impact was significantly greater in the high-nutrient treatments than in the medium- and low-nutrient treatments. However, under high-nutrient conditions the greater impact of *N. albiguttalis* was offset by increased plant productivity so, although the insects inflicted more damage, the plants were still healthier than those exposed to herbivory under lower-nutrient conditions.

Water hyacinth has one of the fastest growth rates of any aquatic plant, where almost all resources are directed into photosynthetic tissues (Howard and Harley 1998). As a result, water hyacinth plants are able to respond rapidly to changes in nutrient conditions and become highly invasive (Coetzee and Hill 2012). In this study, nutrient levels were found to increase water hyacinth plant fitness greatly, as evidenced by increases in petiole length, petiole diameter and daughter plant production, compared with medium- and low-nutrient treatments. When nutrients are reduced, water hyacinth plants are considerably less productive, through a loss in photosynthetic activity (Yang et al. 2003). The ability of *N. albiguttalis* to suppress water hyacinth through larval feeding will depend on its ability to overcome plant productivity. Although *N. albiguttalis* was damaging to water hyacinth under high-nutrient treatments, the vigorous growth under these conditions resulted in significantly healthier, albeit damaged, plants than undamaged plants that were grown under lower-nutrient conditions.

While the greatest impact of *N. albiguttalis* was recorded in high-nutrient treatments, there were some impacts at lower-nutrient concentrations that may have important consequences for management, including an increase in the number of daughter plants under low- and medium-nutrient conditions. This may be explained by a shift towards greater reproductive effort due to plant stress (Agrawal 2000). An unexpected result was the increase in wet weight biomass caused by herbivory under medium- and low-nutrient conditions. However, this can be attributed to waterlogging of petioles after mining by *N. albiguttalis* larvae. Plants in medium- and low-nutrient treatments had shorter petioles than those grown in the high-nutrient treatments. Since these were not suitable for *N. albiguttalis* to complete their life cycle in, larvae migrated to a number of other petioles, increasing the proportion of petioles mined. *Niphograpta albiguttalis* is therefore expected to bring water hyacinth to an acceptable level of control in oligotrophic water bodies, although complete control is unlikely to be achieved unless other biological control agents are also present.

The success of biological control of water hyacinth in southern Africa is limited due to the high levels of eutrophication in many of the country's water bodies (Hill and Olckers 2001; Coetzee and Hill 2012). The vigorous growth of water hyacinth under high-nutrient conditions compensates for the damage done by biological control agents, and therefore an acceptable degree of control is often not achieved (Center and Dray 2010). In oligotrophic systems plants cannot compensate, and so acceptable control is often achieved using biological control alone (Hill 2003). The data from this study suggest that *N. albiguttalis* will most likely have a similar impact to that of other water hyacinth biological control agents, including *N. eichhorniae* and *N. bruchi* (Heard and Winterton 2000), *E. catarinensis* (Coetzee et al. 2007) and the mite *Orthogalumna terebrantis* (Marlin et al. 2013), which also inflict more damage on plants grown in higher-nutrient levels, but not enough to overcome the increased vigour of the plant under those conditions. *Niphograpta albiguttalis* is therefore a suitable biological control agent for the eutrophic water systems that occur in southern Africa, and for other countries with comparably eutrophied water systems, but the damage inflicted by *N. albiguttalis* alone will not result in an acceptable level of control.

Physico-chemical parameters of water can be regarded as the most important ecological factors influencing the presence and occurrence of aquatic weeds and thus are a force driving their invasive potential (Sletten and Larson 1984; Gophen 1990; Howard and Harley 1998). It is therefore necessary to assess whether or not biological control is viable, when these bottom-up factors could be overriding any impact from top-down herbivory (Center and Dray 2010). In addressing the influence of these abiotic factors, it is important to consider biological control not as a stand-alone solution, but rather as part of an integrated management strategy using both bottom-up and top-down approaches (Gophen 1990; Hunter and Price 1992; Hill and Coetzee 2008; Center and Dray 2010; van Ginkel 2011). The South African Department of Water Affairs (DWA) has already developed a number of management strategies to work with biological control, including the establishment of minimal standards of effluent discharges, minimising products with high nutrients and the dredging of sediment (Walmsley 2003). However, at present, most management strategies employ a combination of biological and herbicidal control (Hill et al. 2012).

For an integrated management plan using *N. albiguttalis* to be successful in controlling water hyacinth, it must consider the moth's compatibility with herbicides, interaction with other biological control agents, and performance under different nutrient conditions (Center et al. 1999; Hill et al. 2012). Hill et al. (2012) found that, at certain levels, many of the herbicides used to control water hyacinth can be lethal to biological control agents, specifically *E. catarinensis* and *N. eichhorniae*. Therefore, research is needed to determine the tolerance of *N. albiguttalis* specifically to glyphosate-based herbicides, which form the basis of the chemical control programme against water hyacinth in South Africa (Hill et al. 2012). Further studies are needed to examine the species interactions between *N. albiguttalis* and the additional biological control agents of water hyacinth. Weyl and Hill (2012) found that certain biological control agents on water hyacinth interact negatively with one another and therefore have reduced performances when feeding on the same plant.

Overall, the results of this study suggest that, although *N. albiguttalis* contributes to the suppression of water hyacinth under high-nutrient conditions, ultimately the degree of control achieved will not be acceptable. Conversely, despite low-nutrient conditions, under which *N. albiguttalis* may fail to establish or will be less damaging, this species may nonetheless contribute to more acceptable levels of control if used in combination with other biological control agents.

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