Impact of nutrients and herbivory by *Eccritotarsus catarinensis* on the biological control of water hyacinth, *Eichhornia crassipes*

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Abstract

Many water hyacinth infestations in South Africa are the symptom of eutrophication, and as a result, biological control of this weed is variable. This study examined the effects of herbivory by the mirid, *Eccritotarsus catarinensis*, on water hyacinth grown at high, medium and low nitrogen (N) and phosphorus (P) nutrient concentrations. Water nutrient concentration appears to be the overriding factor affecting plant growth parameters of water hyacinth plants—at high nutrient concentrations, leaf and daughter plant production were more than double than at low nutrient concentrations, while stem length was twice as great at high nutrient concentrations compared to low concentrations. Chlorophyll content was also twice as high at high nutrient concentrations than low concentrations. Conversely, flower production at high nutrient concentrations was less than half that at low concentrations. Herbivory by *E. catarinensis* did not have as great an effect on water hyacinth vigour as nutrient concentration did, although it significantly reduced the production of daughter plants by $23 \pm 9\%$, the length of the second petiole by $13 \pm 5\%$, and chlorophyll content of water hyacinth leaves by $15 \pm 6\%$. In terms of insect numbers, mirids performed better on plants grown under medium nutrient conditions (99 ± 28 S.E.), compared to high nutrient concentrations (52 ± 27 S.E.), and low nutrient concentrations (25 ± 30 S.E.). Thus, these results suggest that the fastest and most significant reduction in water hyacinth proliferation would be reached by lowering the water nutrient concentrations, and herbivory by *E. catarinensis* alone is not sufficient to reduce all aspects of water hyacinth vigour, especially at very high nutrient concentrations.

1. Introduction

Water hyacinth (*Eichhornia crassipes* (Mart.) Solms) infestation is the biggest biotic threat to water bodies throughout Africa. In South Africa, the results of biological control of this weed are variable, despite the allocation of considerable resources to the programme (Hill and Olckers, 2000). This variability has been attributed to a number of factors, including the hydrology of small water bodies, climate incompatibility of the control agents to South Africa, and eutrophication of water bodies (Hill and Cilliers, 1999). Many of the aquatic ecosystems in South Africa are enriched with nitrates and phosphates, and surveys conducted in the 1970s found that the most severe eutrophication problems, ranking as some of the most extreme in the world, were experienced in the more developed and industrialized areas of South Africa (Toerien et al., 1975). Water hyacinth proliferation is usually closely linked to increases in eutrophication

in these systems (Hill, 1999), and as a result, the effect of feeding by biocontrol agents is insufficient to retard water hyacinth growth (Hill and Cilliers, 1999).

The success of biocontrol programmes on aquatic weeds in South Africa, as exemplified by the impact of control agents on water hyacinth, is without a doubt affected by plant quality, which is in turn determined by the nutrient status of the water that these aquatic weeds grow in (Heard and Winterton, 2000 and Wilson et al., 2006). Water hyacinth growth is directly correlated with nutrient concentrations (Gopal, 1987)—as N and P increase, so too does water hyacinth biomass (Gossett and Norris, 1971, Reddy et al., 1989 and Reddy et al., 1990). Furthermore, studies have shown that the N:P ratio in the water affects the N and P use efficiency by water hyacinth (Reddy et al., 1989 and Reddy et al., 1990). The N and P concentrations at which water hyacinth biomass accumulation, and N and P storage are at a maximum, are classified as hypertrophic in South Africa (Holmes, 1996), reinforcing the fear that water bodies with excessive nutrient loading are at risk to water hyacinth invasion. Although water hyacinth can grow in oligotrophic waters, such as the Upper Shire River in Malawi, the plants are small, and are seldom problematic (Hill et al., 1999a and Hill et al., 1999b). Conversely, eutrophication of Hartebeespoort Dam (North West Province) in South Africa resulted in a massive water hyacinth infestation during the 1970s and 1980s, which has subsequently been reduced through chemical control alone (Ashton et al., 1979). It is essential, therefore, to include aspects of nutrient control in any water hyacinth management plan (Hill and Olckers, 2000).

Many studies have documented the impact of water hyacinth biological control agents on size and density of the individual plants, and on stands of the plants (e.g., Del Fosse, 1978, Center, 1980, Center, 1984 and Center et al., 1999). *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) is one of South Africa's most recent introductions against water hyacinth, so the impact it has in the field is unknown. However, the life cycle, host range (Hill et al., 1999a, Hill et al., 1999b, Stanley and Julien, 1999 and Coetzee et al., 2003) and laboratory impact of *E. catarinensis* are known (Coetzee et al., 2005). From laboratory observations, we knew that the mirid will not kill water hyacinth. However, it is important to know if it can reduce growth of the weed, or if it will stimulate compensation under eutrophic conditions, which typify South African waters.

Weed biocontrol agents generally damage plant tissue, kill roots, flowers and seeds, reducing resources, and therefore plant fitness, which can be measured. *E. catarinensis* is a sap-sucking mirid (Hill et al., 1999a and Hill et al., 1999b). Both adults and nymphs feed gregariously on the under surface of the leaves where they pierce the leaf tissue to feed on the plant sap, causing yellowing and chlorosis of the tissue, as a result of the extraction of chlorophyll, and ultimately, premature leaf death (Hill, 1999). The effects of sap-feeding by *E. catarinensis* on water hyacinth are subtle, compared to herbivory by the two weevil control agents, *Neochetina eichhorniae* and *N. bruchi* (Coleoptera: Curculionidae), and the moth *Niphograpta albiguttalis* (Lepidoptera: Pyralidae) (Center and Van, 1989 and Center et al., 1999). Because water hyacinth presents a problem, particularly in eutrophied impoundments in South Africa, the aim of this study was to determine the effect that mirid herbivory has on water hyacinth growth under different nutrient conditions. The

results will be useful in predicting the outcome of biological control of water hyacinth under different nutrient conditions and informing management decisions about integrated pest management and nutrient amelioration.

2. Methods

To determine the effects of insect feeding on water hyacinth growth at different nutrient concentrations, the weed was grown outdoors in 48 plastic tubs at the University of the Witwatersrand, South Africa. Plants were obtained from stock cultures maintained in plastic pools at the University. The plastic tubs were 51 cm by 40 cm and 28 cm deep, filled with 23 L of tap water. Four free-floating healthy water hyacinth plants were placed into each tub, and all dead leaves and stems were removed from the plants. The tubs were then divided into two herbivory treatments—half the tubs were exposed to herbivory by the mirid (experiment), while the other half remained mirid free (control).

High, medium and low nutrient treatments were set up according to concentration concentrations determined by Reddy et al., 1989 and Reddy et al., 1990 to be significant for water hyacinth growth. 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), 5.5 mg N L^{-1} with 1.06 mg P L^{-1} (medium), and 0.5 mg N L^{-1} with 0 mg P L^{-1} (low). Both high and medium treatments are classed as hypertrophic levels by Holmes (1996). The high nutrient treatment matches the concentration of N and P at which maximum N storage occurs in water hyacinth, while the medium nutrient treatment is the concentration of N and P at which productivity is a maximum. The low nutrient treatment is oligotrophic, and is the concentration of N that Reddy et al. (1989) used as a low N treatment. No phosphorous was added to the low treatment as Johannesburg tap water already contains traces of phosphorous (<0.2 mg P L^{-1}). Commercial iron chelate (13% Fe) was also added to all treatments at a concentration of 11.2 mg Fe L^{-1} of water. The nutrient medium was replaced completely at weekly intervals. Each nutrient treatment was replicated eight times for both the experiment and the control, resulting in 24 experimental tubs and 24 control tubs, arranged in a completely randomized design.

The water hyacinth plants were cultivated at these nutrient concentrations for 4 weeks. After this period, all daughter plants and dead leaves and stems were again removed from the plants. All four plants within each tub were then weighed. Fifteen mirids per plant were released onto the experimental water hyacinth tubs (60 insects per tub), while no mirids were released onto the control plants. All the plastic tubs were enclosed by a net canopy (0.8 mm × 0.5 mm mesh size).

Thereafter, plants were sampled weekly for 8 weeks, and the following growth parameters were measured on each plant in every tub: number of leaves, number of daughter plants, number of flowers, maximum petiole length, and the length of the second youngest petiole (leaf 2 petiole). The longest petiole and the second petiole measured were not necessarily the same petioles at consecutive weeks due to new leaf production by the plants. Relative chlorophyll content of the fourth leaf of each plant was measured using a Minolta SPAD-502 chlorophyll meter. Each of these measures was averaged to obtain a mean response per tub, per week.

Insect feeding damage was also recorded on the experimental plants by grading the fourth leaf on each plant from 0 to 5 based on surface area damage, on both the adaxial and abaxial surfaces (where 0 = 0% leaf surface area damaged, 1 = <5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, and 5 = 75–100%). Feeding intensity was also scored from zero to five where one represented little speckling, and five indicated a breakdown of chlorophyll to the point where the leaf appeared yellow/white (Hill et al., 2000). These data were also averaged giving a mean feeding intensity and surface area damage score per tub, per week. During the course of the experiment, two low experiment tubs were lost (one in the fifth week and one in the final week), and one high control tub was lost during the seventh week.

Differences in the mean growth parameters between nutrient and herbivory treatments, at the end of the sample period (week 8), were highlighted using two-factor ANOVAs, and Fisher LSD post hoc comparisons. Linear regressions were performed only on those growth parameters where mirid herbivory had a significant effect, to describe the temporal development over the course of the experiment, emphasizing the differences in nutrient and herbivory treatments.

Kruskal–Wallis ANOVAs were used to illustrate differences in feeding damage between the nutrient treatments at the end of the sample period, while polynomial regressions described the temporal development of these relationships, over the course of the experiment.

At the end of the experiment, the number of mirids collected from each tub was counted. Because these data approximated the lognormal distribution, a one-way ANOVA using a generalized nonlinear model determined whether there was any significant difference in the number of mirids obtained for each treatment. The fresh weight of all the plants in each tub at the end of the sample period was obtained, and the difference in fresh weight at the beginning and at the end of the experiment was calculated for the plants at each nutrient treatment. A Kruskal–Wallis ANOVA determined whether there was a significant difference in fresh weight increase, between plants that had and had not been fed upon, across the nutrient treatments.

3. Results

3.1. Effect of nutrient treatment on plant growth parameters

Water hyacinth growth parameters were affected more by nutrient treatment than herbivory. The number of leaves and daughter plants produced were significantly greater (Fig. 1a and b), the number of flowers produced were significantly fewer (Fig. 1c), both maximum petiole length and length of the second petiole were significantly longer (Fig. 1d and e), and chlorophyll content was significantly higher (Fig. 1f), when the high nutrient treatment was compared to the medium treatment, and the medium nutrient treatment was compared to the low nutrient treatment (Table 1). Furthermore, the difference in plant fresh weight was significant across the nutrient treatments ($H_{(2,46)} = 21.6$, $P = 0.0015$) (Fig. 1g).
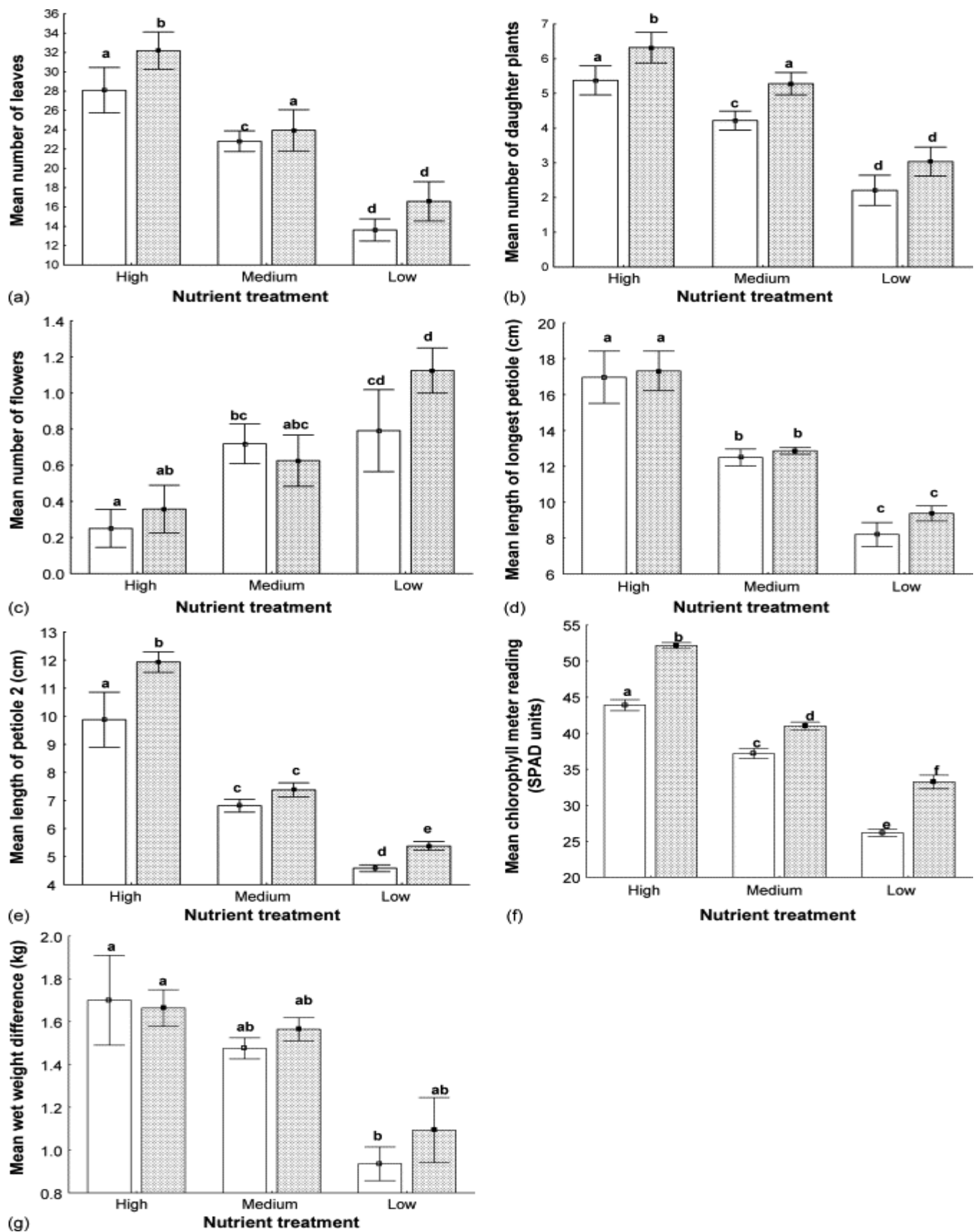
Fig. 1. Differences in water hyacinth growth parameters between herbivory treatments at the end of the 8-week experiment, under high, medium and low nutrient conditions for: (a) number of leaves, (b) number of daughter plants, (c) number of flowers, (d) maximum petiole length, (e) length of second petiole, (f) SPAD chlorophyll meter reading, and (g) difference in plant fresh weight. Clear bars represent the herbivory treatment, shaded bars represent the control. Error bars represent the standard error of the mean. Means compared by factorial ANOVA; those followed by the same letter are not significantly different (Fisher LSD, $P > 0.05$).

3.2. Effect of mirid herbivory on plant growth parameters

By the end of the sample period, there were no significant differences in the number of water hyacinth leaves (Fig. 1a) or flowers (Fig. 1c) produced, or the maximum petiole length (Fig. 1d), between the herbivory treatments, at any of the nutrient concentrations (Table 1). The difference in plant fresh weight was also not significant between plants that had and had not been fed upon ($H_{(1,46)} = 0.2$, $P = 0.63$) (Fig. 1g). However, plants that had been fed upon by the mirid had significantly fewer daughter plants (Fig. 1b), shorter leaf 2 petioles (Fig. 1e), and lower chlorophyll content (Fig. 1f) than plants that had not been subjected to herbivory (Table 1). Fig. 2a–c illustrate the temporal progression of these parameters, respectively, highlighting the greater rate of increase of those not subjected to herbivory. The only significant interaction between nutrient treatment and herbivory was evident for chlorophyll content of water hyacinth leaves (Table 1).

Table 1.

F-statistics and *P* values of the two-way ANOVAs, revealing significant differences in herbivory by *Eccritotarsus catarinensis*, and nutrient treatment, at the end of the 8-week sample period

| Plant growth parameter	Source of variation		
	Nutrient treatment (2,39)	Herbivory (1,39)	Nutrient treatment × herbivory (2,39)
Leaf production	20.1, $P = 0.000$	1.7, $P = 0.21$	0.6, $P = 0.530$
Daughter plant production	32.8, $P = 0.000$	8.4, $P = 0.006$	0.1, $P = 0.956$
Flower production	0.8, $P = 0.000$	1.0, $P = 0.315$	1.2, $P = 0.320$
Maximum petiole length	47.0, $P = 0.000$	0.8, $P = 0.367$	0.1, $P = 0.867$
Leaf 2 petiole length	75.0, $P = 0.000$	8.2, $P = 0.007$	1.4, $P = 0.25$
Chlorophyll	329.4, $P = 0.000$	124.5, $P = 0.000$	5.6, $P = 0.007$

Numbers in brackets are the degrees of freedom for each source of variation.
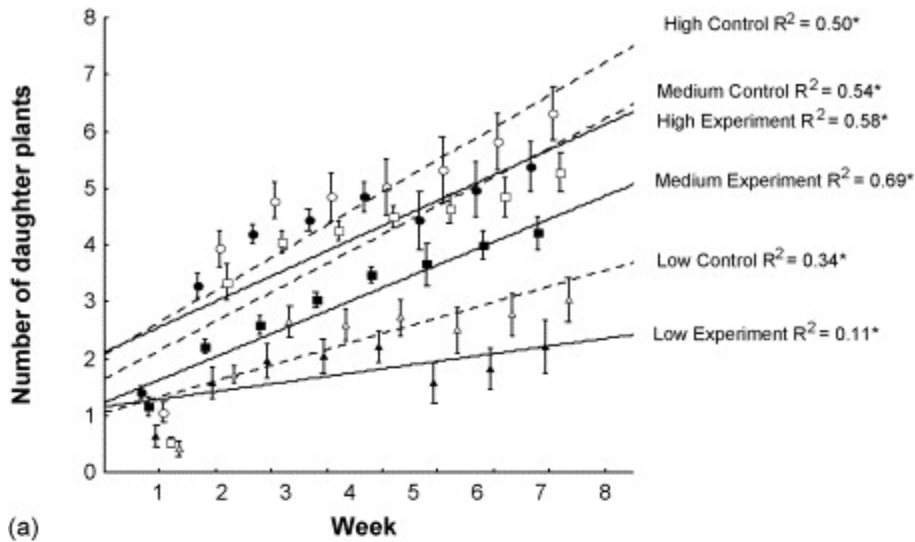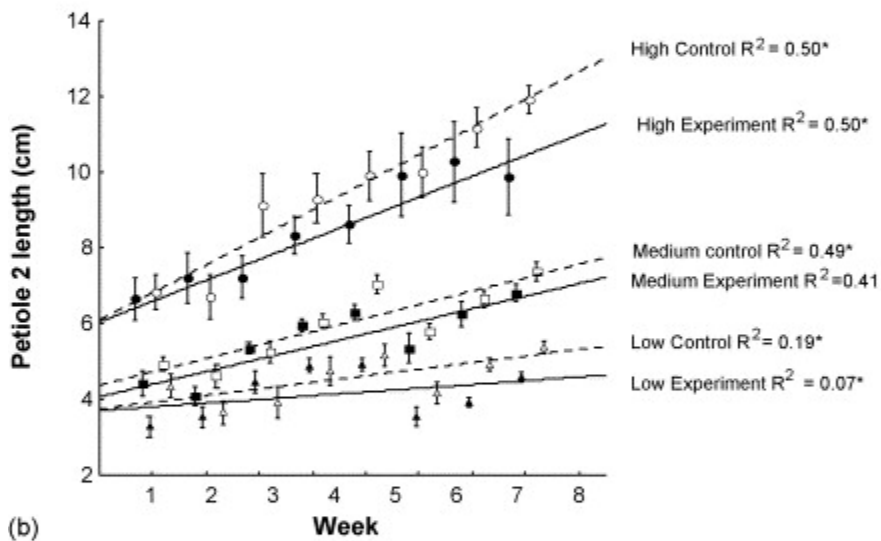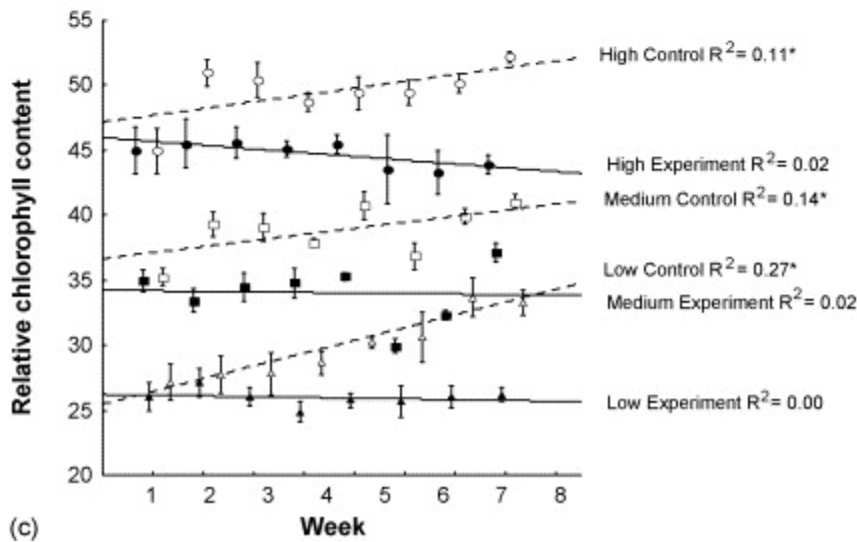
Fig. 2. Increases in (a) the number of water hyacinth daughter plants, (b) length of the second petiole and (c) SPAD chlorophyll meter readings, over 8 weeks, at three different nutrient treatments, either exposed to or not exposed to herbivory by the mirid *Eccritotarsus catarinensis*. Error bars represent the standard error of the mean. [*]$P < 0.05$.

3.3. Feeding damage

At the end of the 8-week sample period, there was no significant difference in feeding damage inflicted by the mirid to water hyacinth leaves between nutrient treatments (surface area $H_{(2,22)} = 3.3$, $P = 0.19$; feeding intensity $H_{(2,22)} = 1.8$, $P = 0.40$). Fig. 3a and b illustrate the relationships between feeding intensity score and surface area damage score, respectively, with time. Even though not significant, feeding damage at week 8 was highest for plants grown at the medium nutrient concentration, followed by the low nutrient concentration, and lowest for plants grown at the high nutrient concentration. Feeding damage declines at a fast rate at the high treatment, with a corresponding increase in leaf production (Fig. 1a), diluting the effects of mirid herbivory, while poor plant quality may explain the decline in feeding damage at the low treatment.
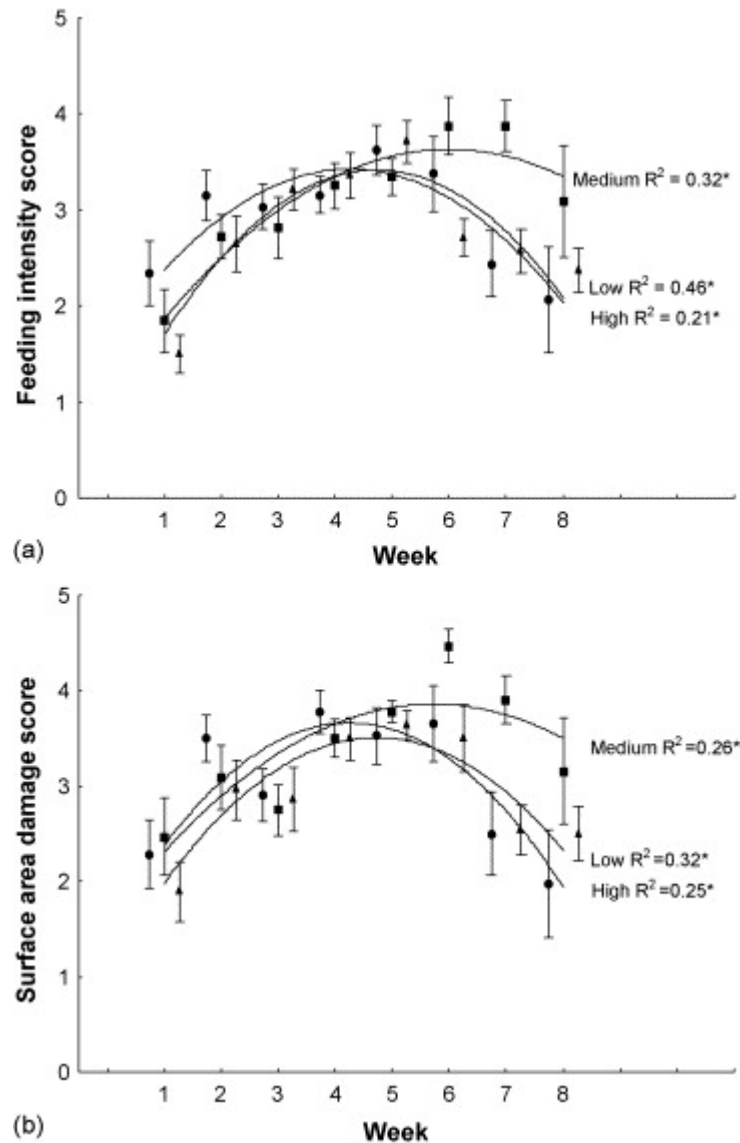

Fig. 3. Polynomial regressions of (a) surface area damaged through feeding (high $y = 1.46 + 1.04x - 0.12x^2$, medium $y = 1.58 + 0.80x - 0.07x^2$, low $y = 1.05 + 1.04x - 0.11x^2$) and (b) feeding damage as indicated by feeding intensity by *E. catarinensis* (high $y = 1.63 + 0.85x - 0.10x^2$, medium $y = 1.09 + 0.85x - 0.07x^2$, low $y = 0.66 + 1.17x - 0.12x^2$), on the third leaf of water hyacinth plants, over 8 weeks. Error bars represent the standard error of the mean. *$P < 0.05$.

The number of insects removed from the tubs at the end of the experiment approximated the lognormal distribution. Significantly more mirids were collected from the medium nutrient treatment (99 ± 28 S.E.), followed by the high nutrient treatment (52 ± 27 S.E.), and then the low nutrient treatment (25 ± 30 S.E.) (Wald $X^2 = 313.3$, $P = 0.000$). Furthermore, the average number of mirids collected in the high and low treatment tubs at the end of the experiment was considerably less than the starting populations of 60 mirids per tub. This is reflected in the lower feeding damage scores for the high and low treatments (Fig. 3a and b).

To summarise, water nutrient concentration appears to be the overriding factor affecting plant growth parameters of water hyacinth plants, although herbivory had some significant effects, primarily on the production of daughter plants, length of the second petiole, and chlorophyll content of water hyacinth leaves, independent of nutrient concentration.

4. Discussion

The results of these nutrient trials are comparable to the findings of other studies (e.g., Gossett and Norris, 1971, Reddy and DeBusk, 1984, Reddy et al., 1989, Reddy et al., 1990 and Wilson et al., 2006) in that water nutrient concentration clearly influenced water hyacinth growth. The higher the nutrient concentration of N and P, the more the water hyacinth plants proliferated, in terms of leaf, daughter plant and flower production, and increases in petiole length and chlorophyll content. In addition, the results for petiole length, both longest and second leaf, suggest that low nutrient plants were kept in a juvenile state with short, stout bulbous petioles, while high nutrient plants shifted to more of an adult phase with longer, more narrow petioles.

On the other hand, herbivory by *E. catarinensis* did not have as great an effect on water hyacinth vigour as water nutrient content did. Only certain water hyacinth characteristics were significantly suppressed by herbivory (Table 1), chlorophyll content being the most dramatic. The mirid removed considerable amounts of chlorophyll through the extraction of sap, over the study period.

Over a longer sample period, mirid herbivory might have had a greater effect on water hyacinth growth, as the mirid population increased, thereby inflicting more damage. Mirids take 23 days to develop from egg to adult, and adult longevity is approximately 50 days, at 25 °C (Hill et al., 1999a and Hill et al., 1999b), so the 8-week sample period in this study was not long enough to allow the mirid populations to increase to a level where they would significantly affect water hyacinth vigour. For example, even though mirid herbivory did not significantly reduce leaf production, in all of the nutrient treatments, the number of leaves was always lowest in the herbivory trials (Fig. 1a). Even though the initial number of mirids used to inoculate the plants is comparable to numbers of mirids found on plants in the field, inoculating the treatments with more insects might have also enhanced their effects on water hyacinth vigour.

Herbivory affected water hyacinth plant growth parameters by significantly reducing the number of daughter plants produced per plant, rather than the number of leaves produced or the weight of the plant. This is consistent with the findings of Heard and Winterton (2000), who found that weevil herbivory influenced daughter plant production, rather

than the mass or number of leaves produced by water hyacinth plants. Water hyacinth populations increase rapidly by vegetative reproduction through the production of daughter plants (Edwards and Musil, 1975) so any reduction in daughter plant production will have negative consequences for the rate of spread of water hyacinth, and consequently, its competitive ability (Coetzee et al., 2005).

Although feeding damage by the mirid did not directly affect a number of the growth parameters measured in this study, there may be other less obvious affects occurring, that compromise water hyacinth vigour. For example, feeding damage caused by the mirid may facilitate the dissemination and transmission of microbial pathogens already released against the weed, and hemipteran stylet scars may provide entry sites for these pathogens (Galbraith, 1984). The effects of insect damage could also be compounded by subsequent invasion by facultative and saprophytic organisms that cause decay of the plant (DeLoach and Cordo, 1978). It has been suggested that tunneling by *N. eichhorniae* larvae may provide a route of entry for pathogens, particularly micro-organisms and fungi (Evans and Reeder, 2000). Moran (2005) found that augmentation with both water hyacinth weevils and the fungal pathogen *Cercospora piaropi* Tharp led to the development of an additive biological control impact on water hyacinth. Furthermore, the water hyacinth mite, *Orthogalumna terebrantis* Wallwork feeds in the wounds caused by feeding damage of other water hyacinth control agents, such as the weevils and *N. abiguttalis* (Cordo and DeLoach, 1975 and Cordo and DeLoach, 1976). Feeding damage caused by *E. catarinensis* might also facilitate feeding damage by the mite.

Populations of herbivorous insects often increase in response to plants growing under eutrophic conditions (Room, 1990), but in this study it appears that rapid water hyacinth leaf production at high nutrient concentrations counteracted the adverse effects of herbivory by *E. catarinensis*. Both Heard and Winterton (2000) and Wilson et al. (2006) found that population growth rate of *N. bruchi* and *N. eichhorniae*, respectively, was faster at higher nutrient concentrations, whereas, this study yielded fewer mirids at the highest nutrient treatment, compared to the medium nutrient treatment. Furthermore, feeding damage to the plants was higher at medium nutrient concentrations than high nutrient concentrations (although not significant), perhaps because of increased production of leaves at high nutrient concentrations, which may have obliterated the effects of herbivory by *E. catarinensis*. Alternately, there is some evidence that compounds found within the leaves of water hyacinth (namely phenolics) might act as a deterrent to herbivore attack and that the concentractions of these compounds increase when the plant is grown in high N and P environments (Center and Wright, 1991). Whilst this might explain why *E. catarinensis* performed badly under the high nutrient regimes, it was not investigated in this study.

The differences in insect performance between this study, and those of Heard and Winterton (2000) and Wilson et al. (2006), besides the fact that different insects were used, might result from different experimental water nutrient concentrations, which correspondingly affected plant nutrient content. The high nutrient treatment in this study was more than 10-fold higher than either high nutrient concentration used in their studies, while the medium treatment was slightly higher than their high treatments. Furthermore, the low nutrient treatment in this study was comparable to Heard and Winterton's (2000) medium treatment and Wilson et al. (2006) low treatment. Therefore, the higher numbers

of mirids collected from the medium nutrient treatments in this study are comparable to the high population numbers of weevils in their high nutrient treatments.

These findings have important consequences for biocontrol of water hyacinth in South Africa. The concentrations of N and P used in this study are very high, but are realistic values in that they are the threshold concentrations for N storage of water hyacinth, while the medium N and P nutrient concentrations are the thresholds for maximum net plant productivity (Reddy et al., 1989 and Reddy et al., 1990). According to South African Water Quality standards, both the high and medium N and P concentrations are hypertrophic (Holmes, 1996), and impoundments do exist in South Africa with N and P concentrations similar to those of the high treatment in this study. A study conducted at Hammarsdale Dam in the KwaZulu Natal Province concluded that a site close to a wastewater inlet was hypertrophic (1.561 mg N L^{-1} and 0.731 mg P L^{-1}) (Oberholzer, 2002), which is comparable to the medium nutrient treatment used in this study. Both *N. eichhorniae*, established since 1989, and *E. catarinensis*, established since 1996, have reached very high population densities at Hammarsdale Dam but appear to have had little impact on the water hyacinth infestation (Hill and Olckers, 2000). It is predicted that the hypertrophic conditions have negated the effects of herbivory by these two control agents. Establishing *N. bruchi* at this site, which prefer plants with a high nutrient status (Heard and Winterton, 2000), may be only part of the solution to controlling water hyacinth on this dam. According to the results of this study, the fastest and most significant reduction in water hyacinth proliferation would be reached by reducing the nutrient inflow into this impoundment, thereby decreasing its nutrient status, allowing *N. eichhorniae* and *E. catarinensis* to exert a level of control.

The concentrations of the low nutrient treatment in this study are classified as oligotrophic, according to Holmes (1996). Mirid herbivory at the low nutrient treatment affected water hyacinth growth parameters, especially chlorophyll content and daughter plant production, both important parameters for the colonizing ability of the plant. New Years Dam in the Eastern Cape is an oligotrophic impoundment in South Africa where successful biological control of water hyacinth in South Africa has occurred (Hill and Cilliers, 1999). *Neochetina eichhorniae* reduced the infestation to 10% of its original size in 10 years (Hill and Olckers, 2000). *E. catarinensis* was released here in winter in 1996, but failed to establish possibly due to low winter temperatures (Hill and Olckers, 2000). Had it been released in spring, it might have had more time to build up significant population numbers during the warmer months, exerting an additional level of control.

In conclusion, herbivory by *E. catarinensis* alone is not sufficient to reduce all aspects of water hyacinth vigour at very high nutrient concentrations. However, water hyacinth control may be further enhanced by the mirid, in both eutrophic and oligotrophic conditions, on infestations where other control agents have already been released. In addition, mirid feeding differs from other water hyacinth control agents, except the mite, *O. terebrantis*, which also extracts chlorophyll from the leaves, adding another dimension of feeding damage to water hyacinth control.

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