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Nutrient-mediated effects on *Cornops aquaticum* Brünér (Orthoptera: Acrididae), a potential biological control agent of water hyacinth, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae)



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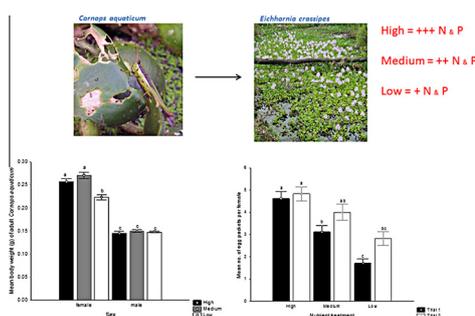
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HIGHLIGHTS

- Host plant quality for phytophagous insects can affect their performance.
- We investigated the effect of variable foliar nitrogen levels on an insect-weed system.
- We found significant effects on grasshopper fecundity, survival, body size and sex ratios.
- The results indicate significant potential for bottom-up regulation of this biocontrol agent.
- Understanding a biocontrol agent's response to plant quality can assist strategic weed management.

GRAPHICAL ABSTRACT



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ABSTRACT

Host plant quality for phytophagous insects, of which nitrogen is one of the most crucial components, is highly variable and can be a major determinant of their performance. This has implications in insect-weed biological control systems where host plant quality can affect establishment, survival and population growth rates of the biocontrol agents. However, an understanding of bottom-up effects on these systems, particularly in aquatic environments which are prone to seasonal fluctuations in nutrient availability, can assist in directing management strategies to achieve the best results. We evaluated nutrient-mediated effects on the performance of a leaf-feeding biocontrol agent, the grasshopper *Cornops aquaticum* for the invasive aquatic weed, water hyacinth *Eichhornia crassipes*. Female *C. aquaticum* and their offspring had higher body weights when fed a high quality diet compared to a diet low in foliar nitrogen. Nymphal survival (high = 82%, medium = 71%, low = 64%) and female fecundity increased with an increase in dietary nitrogen. High and low levels of nutrients caused a shift in the sex ratios, being female-biased on the high quality diet and male-biased on the low quality diet. These results indicate that *C. aquaticum* is highly sensitive to foliar nitrogen, suggesting significant potential for bottom-up regulation of this species. Changes in the abundance and distribution of *C. aquaticum* according to nutrient availability may therefore mediate its impact on the weed. This subsequently highlights the importance of understanding the influence of nutrients on aquatic insect-weed systems and how it can drive decision-making in strategic management programmes.

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1. Introduction

Phytophagous insects are faced with variability in the quality of their host plant, which is linked to environmental conditions and which may positively or negatively influence their performance (Awmack and Leather, 2002), defined as their reproductive potential, survival and growth rates. Both the nutritional value and other constituents of plants, such as secondary defensive metabolites, can have an effect on many aspects of insect behaviour and life history characteristics (Myers and Post, 1981; Taylor, 1984, 1989; Ohmart et al., 1985; Joern and Behmer, 2002; De Bruyn et al., 2002; Hogendorp et al., 2006).

Nitrogen in particular is a critical nutritional element for herbivorous insects and it has been suggested that they are functionally limited by the availability of nitrogen in their diet (White, 1976; Mattson, 1980). Increased nitrogen in plant tissue associated with elevated nitrogen in the environment can have positive effects such as increased survival and body size (De Bruyn et al., 2002; Myers and Post, 1981; Hogendorp et al., 2006). Host plant quality can also have a wide range of effects on the fecundity and reproductive strategies of insects. Within-species fecundity is highly variable and is linked to genetic factors, conditions during immature development as well as prevailing environmental conditions during egg development and oviposition (Honěk, 1993). Potential and realized (achieved) fecundity are also influenced by a wide range of factors and in some cases the difference between the two can be substantial (Awmack and Leather, 2002). Host plant quality available to female phytophagous insects during egg development can have an impact on fitness of their offspring. Some of the indirect effects to insects of increased environmental nitrogen include increases in plant biomass as well as changes in plant defensive chemicals associated with variable nitrogen availability (Bryant et al., 1983, 1987; Gerson and Kelsey, 1999). The effects can vary between generalist and specialist herbivores (Dyer et al., 2004), but environmental nitrogen availability can have a substantial impact on both individual insect performance (Minkenberg and Ottenheim, 1990) and insect population dynamics (Kyttö et al., 1996; Denno et al., 2003; Xhong-xian et al., 2007) as a result of changes in their behaviour and life history characteristics.

There is plasticity in the physiological responses of phytophagous insects to changes in the quality of their diet. These dynamics may influence population abundances of herbivorous insects and for biological control agents, determine their potential to control populations of the target weed. In general, the effects of high plant quality are expected to have a positive effect on the performance of biological control agents (Price, 2000; Van Hezewijk et al., 2008; Wheeler, 2003; Myers and Post, 1981; Room and Thomas, 1985).

Water hyacinth, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae), an aquatic, free-floating perennial herb, is widespread and highly invasive in South Africa where it is considered to be the most prominent economic and environmental aquatic weed. Of the five floating invasive aquatic weeds in the country, *E. crassipes* has had the greatest investment in control measures with comparatively limited success (Coetzee et al., 2011). The success of biological control, which is the only sustainable method for long-term management of *E. crassipes*, is seemingly dependent on a number of factors, particularly the nutrient status of water bodies (Byrne et al., 2010; Coetzee and Hill, 2012). Many of South Africa's water bodies are highly eutrophic, rich in nutrients such as nitrates and phosphates which increase plant biomass production, growth and vegetative reproduction (Reddy et al., 1989, 1990; Ripley et al., 2006; Coetzee et al., 2007, Bownes et al., 2013) to such an extent that aquatic weed problems are considered to be symptomatic of eutrophication. A recent meta-analysis of laboratory studies that investigated the influence of nitrogen and phosphorus on the impact of herbivory by several biological control agents al-

ready released in South Africa and field data, showed that the nutrient status of water bodies has a greater impact on *E. crassipes* growth than the biocontrol agents (Coetzee and Hill, 2012). Although these agents, such as *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), *N. bruchi* Hustache, *Orthogalumna terebrantis* Wallwork (Acarina: Galumnidae) and *Ecritotarsus catarinensis* Carvalho (Hemiptera: Miridae), play an important role in the management of *E. crassipes*, their impact has been highly variable and improved control levels through the classical approach were desirable.

The water hyacinth grasshopper, *Cornops aquaticum* Brünner (Orthoptera: Acrididae) is the most recent *E. crassipes* biocontrol agent introduction in South Africa with the first releases taking place early in 2011 (Bownes and King, 2010). After the release of *E. catarinensis* in 1995, *C. aquaticum* was the most promising candidate agent for South Africa when biocontrol practitioners advocated consideration of new agents due to unsatisfactory levels of control of *E. crassipes* after more than 30 years of biological control. (Hill and Cilliers, 1999; Hill and Olckers, 2001) *C. aquaticum* originates and is distributed throughout the Neotropics, inhabiting lowlands where it is often found in abundance on its host plant, *E. crassipes* (Adis et al., 2007). According to Silveira-Guido and Perkins (1975), *C. aquaticum* is diurnal, bivoltine, overwinter as adults and exhibit a sex ratio of 1:1. The pre-oviposition and incubation periods last 25–30 days, and the nymphs develop for 40–55 days passing through five to seven instars (Oberholzer and Hill, 2001; Adis et al., 2004; Bownes 2009).

Pre-release studies on *C. aquaticum* to predict the effect of nutrient-enrichment on its potential efficacy and feeding rates and on the compensatory ability of *E. crassipes*, showed that increases in nitrogen in the water, and consequently the plant, reduced *C. aquaticum* nymphal feeding rates as well as the impact of herbivory on plant performance (Bownes et al., 2013). However, the link between insect physiology and nutritional ecology or food requirements suggests that host plant quality will also influence the biocontrol potential of *C. aquaticum* through associated population fluctuations of the insect. Thus, as part of an holistic assessment of the effect of plant and water nutrient levels (which are highly correlated) on *C. aquaticum* efficacy, the influence of foliar nitrogen levels on the individual performance of the grasshopper was also investigated, to predict the bottom-up effects on *C. aquaticum* population dynamics. The effect of nitrogen fertilization on the population ecology of biocontrol agents can be predicted through the response of individuals in laboratory studies (Van Hezewijk et al., 2008). This could assist in the strategic management of *E. crassipes* in South Africa, which has recommended an augmentive, integrated approach rather than classical biological control (Coetzee et al., 2011). This paper investigates the effect of plant quality on survival and life history characteristics of *C. aquaticum*. These studies were conducted prior to the release of the grasshopper in South Africa, to estimate the efficacy of the agent before adding it to the ecosystem.

2. Materials and methods

2.1. Nutrient treatments

Foliar nitrogen levels of *E. crassipes* were manipulated by adding different concentrations of nitrates (and phosphates) to the water in which stock plants were cultivated. Water nutrient levels and plant nutrient levels in *E. crassipes* are highly correlated (Gossett and Norris, 1971; Soti and Volin, 2010). Nitrate and phosphate levels were selected to represent a range of nutrient conditions typical of water bodies in South Africa. The selected concentrations (Table 1) are the averages of a year's worth of data from three of 15 sites (Byrne et al., 2010) that represented three different nutrient

Table 1

Concentrations of nitrates and phosphates in mg L^{-1} used to cultivate *Eichhornia crassipes* plants to investigate nutrient-specific responses of *Cornops aquaticum*. The nutrient levels are representative of nutrient levels found in South African river systems and impoundments ranging from highly eutrophic to oligotrophic.

	High (eutrophic)	Medium (eutrophic/mesotrophic)	Low (oligotrophic)
Nitrates (mg L^{-1})	7.6	2.52	0.034
Phosphates (mg L^{-1})	1.37	0.316	0.024

classifications namely eutrophic (herein referred to as the high nutrient condition), mesotrophic/eutrophic (medium nutrient condition) and oligotrophic (low nutrient conditions). The classifications are based on the amount of nitrates in the water in mg L^{-1} according to the South African Water Quality Guidelines (Holmes, 1996). Nitrates and phosphates were manipulated by adding potassium nitrate (KNO_3) and potassium dihydrogen phosphate (KH_2PO_4) respectively to municipal water, according to the concentrations in Table 1. Commercial chelated iron (Mircel FE 130) was also added at a rate according to Coetzee et al. (2007). Plants were cultivated in plastic troughs containing either 15 or 20 L of water, depending on the trial, and the compound weights (g) were adjusted accordingly for the correct levels of nitrates and phosphates. *E. crassipes* plants were obtained from stock cultures and cultivated in the nutrient media for a period of three months before use and the nutrient media were replaced weekly. Water nutrient level served as a proxy for plant quality and Bownes et al. (2013) found highly significant differences in foliar nitrogen levels from plants cultivated at the same nutrient levels tested here. Mean nitrogen content of leaves 3–5 (Penfound and Earle, 1948) of *E. crassipes* plants cultivated at the nutrient concentrations specified above were (1) 3.41, 2.00 and 1.76 N g/dw% in the high, medium and low nutrient treatments, respectively, indicating that adult and nymphal *C. aquaticum* was exposed to different levels of foliar nitrogen in the trials detailed below.

2.2. *C. aquaticum* fecundity and survival

2.2.1. Effect of plant nutrients on fecundity, nymphal survival and body size of adults and their offspring

This trial was conducted in a quarantine glasshouse at the Plant Protection Research Institute (ARC-PPRI) in Pretoria, South Africa. The glasshouse was maintained at 18/30 °C min/max with a day-length of 14 h and the trial was conducted from October to December 2007. Eight female (parental generation) *C. aquaticum* were maintained on *E. crassipes* plants cultured at optimum nutrient levels, provided by a slow release fertilizer, Osmocote®. Twenty-eight of their offspring per nutrient treatment were removed as neonate nymphs and reared to adults on *E. crassipes* plants cultured at the high, medium and low nutrient levels in 20 L plastic troughs. These nymphs were reared in groups on whole, floating *E. crassipes* plants held in rearing boxes (44 × 31 × 34 cm) and were separated into males and females before their final moult to prevent copulation before they were used in the next stage of the trial. After the final nymphal moult, the adult *C. aquaticum* were sexed, weighed on a Mettler Toledo AL54 balance in a 30 ml glass vial with a predetermined weight (g), and paired. Adult pairs were then introduced onto *E. crassipes* plants grown at the same nutrient levels on which the nymphs had been reared. These plants were held in 15 L plastic tubs (43 × 31 × 19 cm) and covered with a net sleeve to prevent the adults from escaping. The nutrient media were replaced weekly throughout the duration of the trial. There were eight pairs of adults in the high and medium nutrient treatments but only se-

ven in the low nutrient treatment due to a shortage of females. The trial ran for a period of six weeks and the total number of egg packets produced per female and the number and body weight (g) of their offspring were recorded for each pair of adults at each nutrient treatment. The number of eggs per egg packet was not recorded during this trial.

2.2.2. Immature or maternal effects of plant quality on fecundity of *C. aquaticum* females?

The results from trial 2.2.1 indicated that plant quality had significant effects on female fecundity and the body size of their offspring. Therefore a second trial was designed to determine whether these differences were a response to plant quality that females were exposed to during their nymphal development or the quality of their host plant during the pre-ovipositional period. The methodology followed the same design as above with the exception that after weighing (as above) and pairing, adult *C. aquaticum* from all three nutrient treatments were introduced onto plants grown at the high nutrient level. Nymphs that were reared on plants grown under high nutrient conditions served as the control and allowing the females to oviposit on tall, healthy *E. crassipes* plants with elongated petioles (Bownes, 2009), eliminated the possibility that a lack of oviposition sites in the low nutrient treatment influenced the number of egg packets per female. The total number of egg packets produced per female was recorded during this trial.

2.2.3. Statistical analysis

Body weights of female *C. aquaticum* from the fecundity and survival trial (2.2.1) were not significantly different ($F_{1,92} = 1.6967$; $P = 0.2002$) from the maternal effects trial (2.2.2) therefore the data sets were combined to analyse the effect of host plant quality on body size of adult *C. aquaticum*. A two-way ANOVA tested for differences in body mass of males and females and for the effect of plant quality on body mass of the two sexes. The pre-oviposition period data were log-transformed to obtain normality and analysed with a one-way ANOVA. The effect of plant quality on the number of egg packets per female and the number of nymphs per egg packet and their body weights (g) (trial 2.2.1) were compared between nutrient treatments using a one-way ANOVA. Tukey's HSD test for unequal sample sizes was used as a post

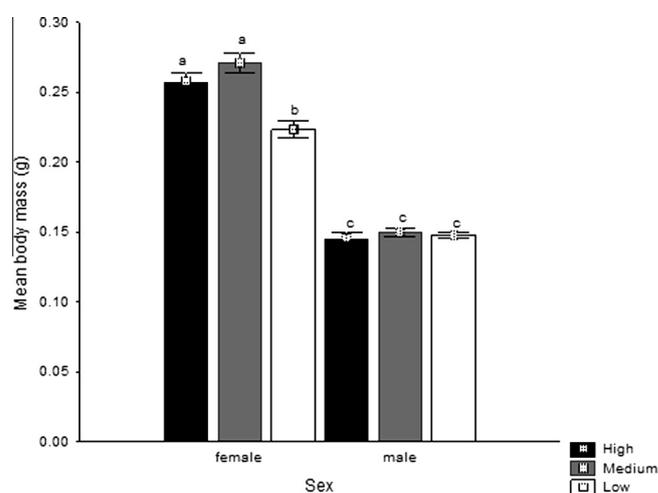


Fig. 1. Mean body mass *Cornops aquaticum* males and females reared on *Eichhornia crassipes* grown at high, medium and low nutrient levels. Means compared by two-way ANOVA; those with the same letter are not significantly different (Tukey's HSD test for unequal sample sizes; $P < 0.05$). Error bars represent the standard error of the mean.

hoc comparison of the means for all ANOVAs (Zar, 1999). All data analyses were done in Statistica (v 6.0., StatSoft, 2001).

3. Results

3.1. Effect of nutrient treatment on body size of nymphs and adults

Nutrient treatment had a significant effect ($F_{2;92} = 10.78$; $P < 0.0001$) (Fig. 1) on body mass of female *C. aquaticum*, with females from the high and medium nutrient treatments weighing 19% and 24% more, respectively, than females reared on low nutrient plants. Body mass of male *C. aquaticum* was not influenced by the quality of their food. Mean body mass of *C. aquaticum* females was significantly greater than males ($F_{1;92} = 539.89$; $P < 0.0001$) (Fig. 1) which was expected due to sexual dimorphism within the species. The interaction between nutrient treatment and sex was highly significant ($F_{2;92} = 9.90$; $P = 0.0001$), hence the effect of food quality was not the same for both sexes. The mean body mass of newly hatched nymphs increased with an increase in plant nutrient supply ($F_{2;16} = 4.678$; $P = 0.025$) but only the high nutrient treatment was significantly different from the low nutrient treatment (Fig. 2).

3.2. Effect of nutrient treatment on nymphal survival

Of the 28 neonate nymphs per treatment reared on *E. crassipes* plants of differing nutritional qualities, 82% survived to adulthood in the high nutrient treatment, 71% in the medium nutrient treatment and only 64% in the low nutrient treatment. Food quality of the nymphs also had an effect on the sex ratios of *C. aquaticum*, with a female to male bias (65:35) in the high nutrient treatment, parity (55 females:45 males) in the medium nutrient treatment and a male bias (39 females:61 males) in the low nutrient treatment.

3.3. Effect of nutrient treatment on female fecundity

The pre-oviposition period of *C. aquaticum* was extended ($F_{2;20} = 5.00$; $P = 0.017$) by more than three days when females were reared and maintained on *E. crassipes* cultivated under low nutrient conditions (Fig. 3). Nutrient treatment had a significant ef-

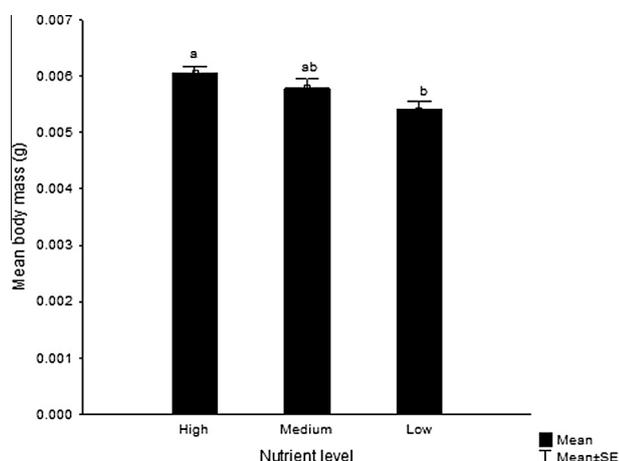


Fig. 2. Mean body mass (g) of neonate nymphs of *Cornops aquaticum* females exposed to *Eichhornia crassipes* grown at high, medium and low nutrient levels during their immature development and pre-oviposition. Means compared by one-way ANOVA, those with the same letter are not significantly different (Tukey's HSD for unequal sample sizes, $P < 0.05$). Error bars represent the standard error of the mean.

fect ($F_{2;20} = 26.058$; $P < 0.0001$) on the fecundity of female *C. aquaticum* reared and maintained after pairing, on whole *E. crassipes* plants grown at high, medium and low nutrient levels (Fig. 4). The number of egg packets produced by females was doubled on high quality plants compared to low quality plants. When switched to high nutrient plants, the number of egg packets produced by females from both low and medium nutrient levels increased, but not significantly (Fig. 4). The mean number of egg packets per female transferred from the low to high nutrient plants was still significantly lower than those of females which had remained on the high nutrient plants throughout their nymphal development and pre-oviposition period. The number of egg packets produced by females in the medium nutrient treatment was not significantly dif-

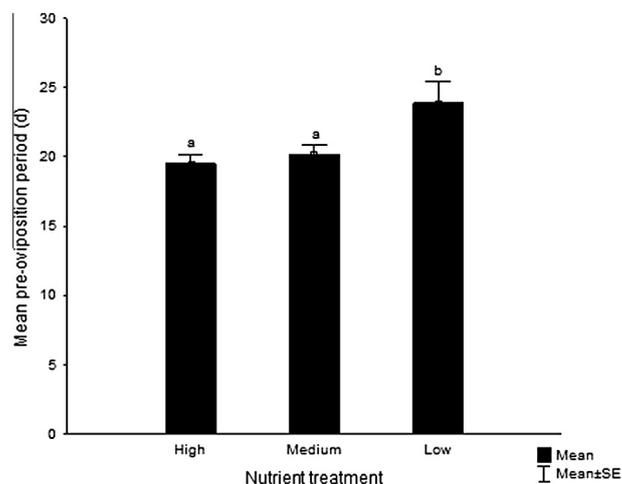


Fig. 3. Mean pre-oviposition periods of female *Cornops aquaticum* reared and maintained on *Eichhornia crassipes* plant grown at high, medium and low nutrient levels (Trial 1). Means compared by one-way ANOVA, those with the same letter are not significantly different (Tukey's HSD for unequal sample sizes, $P < 0.05$). Error bars represent the standard error of the mean.

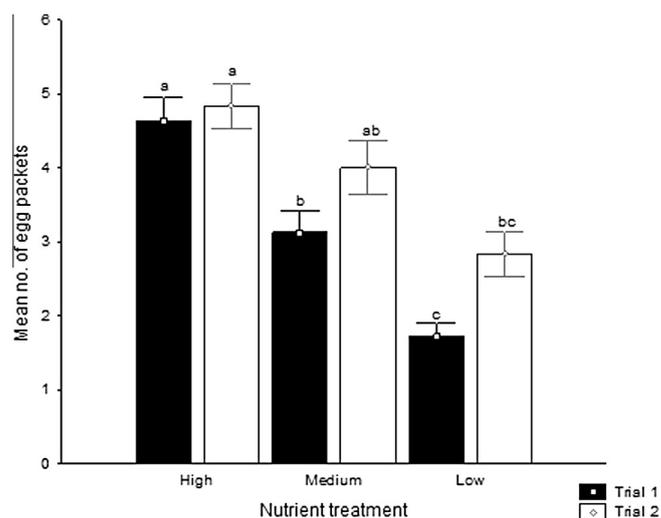


Fig. 4. Mean number of egg packets oviposited by female *Cornops aquaticum* in Trials 1 and 2. Trial 1 females were reared on *Eichhornia crassipes* grown at high, medium and low nutrient levels and transferred at adulthood to plants grown at the corresponding nutrient levels. Trial 2 females were reared on plants grown at high, medium and low nutrient levels and transferred to high nutrient plants at adulthood. Means compared by one-way ANOVA, those with the same letter are not significantly different (Tukey's HSD test for unequal sample sizes, $P < 0.05$). Error bars represent the standard error of the mean.

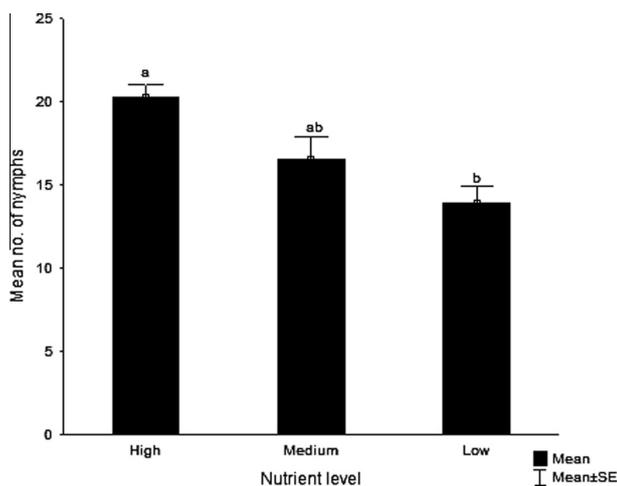


Fig. 5. Mean number of hatched *Cornops aquaticum* nymphs per egg packet of F1 female exposed to *Eichhornia crassipes* grown at high, medium and low nutrient levels during their immature development and pre-oviposition. Means compared by one-way ANOVA, those with the same letter are not significantly different (Tukey's HSD for unequal sample sizes, $P < 0.05$). Error bars represent the standard error of the mean.

ferent from females in the high nutrient treatment when switched to a high quality diet.

Nutrient treatment also had a significant influence ($F_{2,18} = 7.578$; $P = 0.0041$) on the number of nymphs to hatch from egg packets of females that were reared and maintained as adults on different nutrient treatment plants (Fig. 5). Nymphal hatch increased with an increase in plant nutrient supply to *E. crassipes*, but only the high and low nutrient treatments were significantly different from one another.

4. Discussion

4.1. Effect of host plant quality on individual performance of *C. aquaticum*

It is widely known that the nutritional quality of host plants of phytophagous insects is a major determinant of their reproductive capacity and general performance at the individual level. The results reported here showed that variation in the nutritional composition of *E. crassipes* plants, as influenced by water nutrient concentrations, had a significant effect on the life history characteristics of one of its host specific herbivores. Correlative increases in plant nitrogen with increased water nitrate levels (Bownes et al., 2013) elicited increased *C. aquaticum* nymphal survival, higher body weights of adult females and their offspring and increased realized fecundity of females as measured by the number of egg packets and the number of nymphs per egg packet.

Results from the present and past studies on *C. aquaticum*'s life history characteristics (Oberholzer and Hill, 2001; Adis et al., 2004; Capello et al., 2007; Viera and dos Santos, 2003) indicate that this species displays considerable phenotypic plasticity according to temperature, insolation in different geographical areas and food quality (Adis et al., 2004; Capello et al., 2007). For example, the number of nymphal instars can vary between five (Bownes, 2009) and seven (Oberholzer and Hill, 2001) and in one study, the mean development time for nymphs was extended to 122 days (Viera and dos Santos, 2003). Although the number of nymphal instars and total development time of *C. aquaticum* was not affected by the nutritional quality of its host plant (Bownes, 2009), nymphal survival is expected to be strongly influenced by bottom-up effects, as is commonly observed in immature insects developing on high-quality diets with higher levels of nitrogen (Myers and Post,

1981; Fox et al., 1990; De Bruyn et al., 2002; Wheeler, 2003). However, evidence from other studies (Oberholzer and Hill, 2001; Adis et al., 2004; Capello et al., 2007; Viera and dos Santos, 2003) suggest that other factors such as climate will cause variability in *C. aquaticum* nymphal traits in the field in South Africa.

C. aquaticum fecundity and female body size were positively influenced by increasing levels of nitrogen in plant tissue which is a common response of insects to increased concentrations of foliar nitrogen (Ohmart et al., 1985; Hogendorp et al., 2006; Stanley et al., 2007), including orthopterans (Joern and Behmer, 2002; Branson, 2004). It appears that *C. aquaticum* fecundity was influenced by three interacting factors: body size (influenced by nutrient conditions), food quality available to females during their immature development and food quality available during the pre-oviposition period, suggesting the potential for bottom-up regulation of the difference between potential and realized fecundity. Although there were potentially confounding factors such as differences in the number of eggs per egg packet which was not recorded, the number of hatching nymphs is an indication of egg viability, hence the resultant number of offspring per female grasshopper were indeed influenced by foliar nitrogen. The response of female *C. aquaticum* to changes in the quality of their diet from the immature to post-mating development stages suggests the potential for an increase in *C. aquaticum* population growth as a response to increased reproductive potential and survival with nutrient fluxes in the aquatic environment. Center and Dray (2010) demonstrated the effect of the nutrient environment on the reproductive potential of the *Neochetina* weevils and hence the potential for seasonal effects on their reproduction due to the stochastic nature of aquatic systems. Reproductive ability of the weevils increased with nitrogen fertilization, as it did with *C. aquaticum*, indicating that population growth of both species, as a function of reproductive capacity, will be regulated by bottom-up effects.

Food quality is known to influence insect sex ratios, usually being female-biased when food quality is high (Craig et al., 1992) as was found in the present study. Mopper and Whitham (1992) suggest that sex ratios are seldom used to explain insect performance in natural systems, despite the influence of plant quality on this aspect of plant-insect interactions. A shift in sex ratios according to plant nitrogen may be an adaptive, functional response because the reproductive success of insects in terms of female fecundity is closely linked to dietary nitrogen (Mattson, 1980; Awmack and Leather, 2002). Although the sex ratio of *C. aquaticum* is 1:1 in the native range (Silveira-Guido and Perkins, 1975), as it was in the medium nutrient treatment tested here, in theory, life history parameters will be adaptive to maximize productivity through reproduction to produce the highest number of surviving offspring. The effect of plant nutrients on the differential survival rates of male and female *C. aquaticum* suggests that the sex ratio may shift with a change in plant quality with changing environmental nutrient conditions, which would likely have an effect on the potential rate of population increase from generation to generation. Furthermore, due to size sexual dimorphism within the species, with females being considerably larger than males with differential consumption rates (Bownes et al., 2013), the level of control exerted by a population of *C. aquaticum*, under particular nutrient conditions may change with a shift in the sex ratio.

4.2. Implications for biocontrol of *E. crassipes*

The main purpose of this study was to determine individual nutrient-specific responses of *C. aquaticum* in order to predict the population-level effects of the nutrient environment and therefore the implications for biological control. McClay and Balciunas (2005) note that the geographical ranges and abundances of introduced biocontrol agents are primarily functions of their life history

characteristics and their response to the environment. However, extrapolating to the field on the basis of laboratory research can be limited by a lack of knowledge of the response of an agent to all external influences in its environment.

Despite potential shortcomings in accurate predictions of agent success from laboratory studies, Van Hezewijk et al. (2008) showed that it is possible for population-level effects to be successfully predicted on the basis of individual-level responses with the classical biological control agent *Mogulones cruciger* Herbst (Coleoptera: Curculionidae) on houndstongue, *Cynoglossum officinale* L. (Boraginaceae). The following predictions on the performance of *C. aquaticum* as a biocontrol agent for *E. crassipes*, according to its nutrient environment, are based on the present findings and that of Bownes et al. (2013): *C. aquaticum* developing on high-nutrient plants should establish more readily, survive better and have a greater population increase due to increased fecundity and a female-biased sex ratio. This would result in higher population growth rates and higher damage levels due to higher numbers of females. These obvious advantages may be negated to some extent due to lower overall feeding rates and greater compensatory ability of *E. crassipes* under these conditions (Bownes et al., 2013). But with high population growth rates, the time taken to reach population densities that are sufficiently damaging should be significantly reduced. A low quality diet will promote increased feeding rates (Bownes et al., 2013) but a male-biased sex ratio and reduced survival and fecundity will result in lower population growth rates with substantially smaller increases in numbers from generation to generation.

It is further predicted that a combination of *C. aquaticum* and *N. eichhorniae* will be beneficial under mesotrophic/eutrophic nutrient conditions, leading to improved levels of control of the weed. Center and Dray (2010) found that a minimal of 2.1% tissue N concentrations was needed for positive population growth of *N. eichhorniae*, which was released in South Africa in 1974 (Cilliers, 1991) and is the most abundant and widespread biocontrol agent. As was shown here, tissue N levels of approximately 2.0% had positive effects on *C. aquaticum* fecundity and survival which would presumably translate into higher population growth rates under these conditions. From the present and Center and Dray's (2010) study, it appears that plant tissue quality will be a determining factor of the reproductive potential and therefore population dynamics of both species. Other factors such as temperature and insolation, which have been shown to effect life history characteristics of *C. aquaticum* (Capello et al., 2007), as well as *N. eichhorniae* in the field in South Africa (Byrne et al., 2010), will also be major determinants of their establishment success, damage potential and population growth rates. This reinforces the fact that the control potential of *E. crassipes* biocontrol agents will vary according to site-specific biotic and abiotic factors, one of which is undoubtedly host plant quality.

Local environmental manipulation through fertilization to improve biocontrol establishment and success has received some attention during the more recent history of weed biological control (Room and Thomas, 1985; Price, 2000; Wheeler, 2001; 2003; Van Hezewijk et al., 2008). Pest outbreaks in agroecosystems provide a good example of the potential benefits to weed biocontrol in that nitrogen fertilization for improved crop growth is frequently the cause of pest problems and the status of many crop pests increase in response to nitrogen fertilization (Xhong-xian et al., 2007) by creating conditions conducive to population outbreaks of insect species with typically latent population dynamics (Price, 2000). However, Coetzee and Hill (2012) concluded that eutrophic levels of nitrates are more beneficial to *E. crassipes* through increased biomass and growth rates, than they are to their insect biocontrol agents, even those that are known to have higher intrinsic growth rates under these conditions (Heard and Winterton, 2000; Center

and Dray, 2010). So while nitrogen fertilization of aquatic systems would not be advisable, nor necessary in many instances where beneficial levels of nitrogen available to agents such as *C. aquaticum* are already present (Byrne et al., 2010), water quality can be used as a determinant of appropriate management strategies according to known bottom-up and top-down responses of the plant–herbivore system.

In conclusion, the nutritional quality of *C. aquaticum*'s diet has important consequences for its survival and performance, suggesting that bottom-up effects will have a strong influence on the population dynamics of this species, and its control potential. This should have further implications for manipulative management programmes for *E. crassipes* in South Africa where site-specific conditions, release effort and complementary combinations of agents are considered to strategically manage the weed with minimal input and maximum effect. Lastly, the findings have practical applicability to mass rearing *C. aquaticum* for field releases in South Africa. Rearing the grasshopper on vigorous *E. crassipes* plants with a high nitrogen content similar to that tested here, will produce higher numbers of healthy, more fecund individuals for release, which should improve establishment success (Blossey and Hunt, 1999).

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References

- Adis, J., Lhano, M., Hill, M., Junk, W., Marques, M.I., Oberholzer, H., 2004. What determines the number of juvenile instars in the tropical grasshopper *Cornops aquaticum* (Leptysmiinae: Acrididae: Orthoptera)? Stud. Neotropical Fauna Environ. 39, 127–132.
- Adis, J., Bustorf, E., Lhano, M.G., Amedegnato, C., Nunes, A., 2007. Distribution of *Cornops* grasshoppers (Leptysmiinae: Acrididae: Orthoptera) in Latin America and the Caribbean Islands. Stud. Neotropical Fauna Environ. 42, 11–24.
- Awmack, C.S., Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. Annu. Rev. Entomol. 47, 817–844.
- Blossey, B., Hunt, T.R., 1999. Mass rearing methods for *Galerucella clamariensis* and *G. pusilla* (Coleoptera: Chrysomelidae), biological control agents for *Lythrum salicaria* (Lythraceae). J. Econ. Entomol. 92, 325–334.
- Bownes, A., 2009. Evaluation of a plant–herbivore system in determining potential efficacy of a candidate biological control agent, *Cornops aquaticum* for water hyacinth, *Eichhornia crassipes*. PhD Thesis, Rhodes University, Grahamstown.
- Bownes, A., Hill, M.P., Byrne, M.J., 2013. The role of nutrients in the responses of water hyacinth, *Eichhornia crassipes* (Pontederiaceae) to herbivory by a grasshopper, *Cornops aquaticum* Brünner (Orthoptera: Acrididae). Biological Control. 67, 555–562.
- Bownes, A., King, A., 2010. High hopes for water hyacinth hoppers in South Africa. Biocontrol News Info. 32, 1.
- Branson, D.H., 2004. Relative importance of nymphal and adult resource availability for reproductive allocation in *Melanoplus sanguinipes* (Orthoptera: Acrididae). J. Orthoptera Res. 13, 239–245.
- Bryant, J.P., Chapin III, F.S., Klein, D.R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40, 357–368.
- Bryant, J.P., Clausen, T.P., Reichardt, P.B., McCarthy, M.C., Werner, R.A., 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix (*Christoneura conflictana* (Walker)). Oecologia 73, 513–517.
- Byrne, M.J., Hill, M.P., Robertson, M., King, A., Jadhav, A., Katembo, N., Wilson, J., Brudvig, R., Fisher, J., 2010. Integrated Management of Water Hyacinth in South Africa: Development of an integrated management plan for water hyacinth control, combining biological control, herbicidal control and nutrient control, tailored to the climatic regions of South Africa. Report to the Water Research Commission. WRC Report No. No TT 454/10. Water Research Commission, Pretoria.
- Capello, S., Adis, J., de Wysiecki, M.L., 2007. Temperatura y fotoperiodo: qué influencia ejercen en el desarrollo ninfal de *Cornops aquaticum* (Orthoptera: Acrididae)? Amazoniana XIX, 209–216.
- Center, T.D., Dray Jr., F.A., 2010. Bottom-up regulation of water hyacinth weevil populations: do the plants regulate the insects? J. Appl. Ecol. 47, 329–337.
- Cilliers, C.J., 1991. Biological control of water hyacinth, *Eichhornia crassipes* (Pontederiaceae) in South Africa. Agric. Ecosyst. Environ. 37, 207–217.

- Coetzee, J.A., Hill, M.P., 2012. The role of eutrophication in the biological control of water hyacinth, *Eichhornia crassipes*, in South Africa. *Biocontrol* 57, 247–261.
- Coetzee, J.A., Byrne, M.J., Hill, M.P., 2007. Impact of nutrients and herbivory by *Eccritotarsus catarinensis* on the biological control of water hyacinth, *Eichhornia crassipes*. *Aquat. Bot.* 86, 179–186.
- Coetzee, J.A., Hill, M.P., Byrne, M.J., Bownes, A., 2011. A review of the biological control programmes on *Eichhornia crassipes* (C. Mart.) Solms (Pontederiaceae), *Salvinia molesta* D.S. Mitch. (Salviniaceae), *Pistia stratiotes* L. (Araceae), *Myriophyllum aquaticum* (Vell.) Verdc. (Haloragaceae) and *Azolla filiculoides* Lam. (Azollaceae) in South Africa. *Afr. Entomol.* 19, 451–468.
- Craig, T.P., Price, P.W., Itami, K.J., 1992. Facultative sex ratio shifts by a herbivorous insect in response to variation in host plant quality. *Oecologia* 92, 153–161.
- De Bruyn, L., Scheirs, J., Verhagen, R., 2002. Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia* 130, 594–599.
- Denno, R.F., Gratton, C., Döbel, H., Finke, D.L., 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84, 1032–1044.
- Dyer, L.A., Letourneau, D.K., Dodson, C.D., Tobler, M.A., Stireman, J.O., Hsu, A., 2004. Ecological causes and consequences of variation in defensive chemistry of a Neotropical shrub. *Ecology* 85, 2795–2803.
- Fox, L.R., Eisenbach, D.K., Letourneau, J., Van Nouhuys, S., 1990. Parasitism and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. *Oecologia* 83, 414–419.
- Gerson, E.A., Kelsey, R.G., 1999. Piperidine alkaloids in nitrogen fertilized *Pinus ponderosa*. *J. Chem. Ecol.* 25, 2027–2039.
- Gossett, D.R., Norris, W.E., 1971. Relationship between nutrient availability and content of nitrogen and phosphorus in tissues of the aquatic macrophyte, *Eichhornia crassipes* (Mart.) Solms. *Hydrobiologia* 38, 15–28.
- Heard, T.A., Winterton, S.L., 2000. Interactions between nutrient status and weevil herbivory in the biological control of water hyacinth. *J. Appl. Ecol.* 37, 117–127.
- Hill, M.P., Cilliers, C.J., 1999. A review of the arthropod natural enemies, and factors that influence their efficacy, in the biological control of water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae) in South Africa. *Afr. Entomol. Memoir* 1, 103–112.
- Hill, M.P., Olckers, T., 2001. Biological control initiatives against water hyacinth in South Africa: constraining factors, success and new courses of action. In: Julien, M.H., Hill, M.P., Center, T.D., Jianqing, D. (Eds.), Proceedings of the Second Meeting of the Global Working Group for the Biological and Integrated Control of Water Hyacinth. ACIAR, Australia, pp. 33–38.
- Hogendorp, B.K., Cloyd, R.A., Swiader, J.M., 2006. Effect of nitrogen fertility on reproduction and development of citrus mealybug, *Planococcus citri* Risso (Homoptera: Pseudococcidae), feeding on two colours of Coleus, *Solenostemon scutellarioides* L. Codd. *Environ. Entomol.* 35, 201–211.
- Holmes, S., 1996. South African Water Quality Guidelines. World Wide Web. <www.dwaf.gov.za/IWQS/wq_guide/index.html>.
- Honěk, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66, 483–492.
- Joern, A., Behmer, S.T., 2002. Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. *Ecol. Entomol.* 23, 174–184.
- Kytö, M., Niemelä, P., Larsson, S., 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75, 148–159.
- Mattson, W.J., 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* 11, 119–161.
- McClay, A.S., Balcunas, J.K., 2005. The role of pre-release efficacy assessment in selecting classical biological control agents for weeds – applying the Anna Karenina principle. *Biol. Control* 35, 197–207.
- Minkenber, O.P.J.M., Ottenheim, J.J.G.W., 1990. Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. *Oecologia* 83, 291–298.
- Mopper, S., Whitham, T.G., 1992. The plant stress paradox: effects on pinyon sawfly sex ratios and fecundity. *Ecology* 73, 515–525.
- Myers, J.H., Post, B.J., 1981. Plant nitrogen and fluctuations of insect populations: a test with the cinnabar moth – tansy ragwort system. *Oecologia* 48, 151–156.
- Oberholzer, I.G., Hill, M.P., 2001. How safe is the grasshopper *Cornops aquaticum* for release on water hyacinth in South Africa. In: Julien, M.H., Hill, M.P., Center, T.D., Jianqing, D. (Eds.), Proceedings of the Second Meeting of the Global Working Group for the Biological and Integrated Control of Water Hyacinth. ACIAR, Australia, pp. 82–88.
- Ohmart, C.P., Stewart, L.G., Thomas, J.R., 1985. Effects of nitrogen concentrations of *Eucalyptus blakelyi atomaria* (Coleoptera: Chrysomelidae). *Oecologia* 68, 41–44.
- Penfound, W.T., Earle, T.T., 1948. Biology of the water hyacinth. *Ecol. Monogr.* 18, 447–472.
- Price, P.W., 2000. Host plant resource quality, insect herbivores and biocontrol. In: Spencer, N.R. (Ed.), Proceedings of the X International Symposium on Biological Control of Weed. Montana State University, Montana, pp. 583–590.
- Reddy, K.R., Agami, M., Tucker, J.C., 1989. Influence on nitrogen supply rates on growth and nutrient storage by water hyacinth (*Eichhornia crassipes*) plants. *Aquat. Bot.* 36, 33–43.
- Reddy, K.R., Agami, M., Tucker, J.C., 1990. Influence of phosphorus on growth and nutrient storage by water hyacinth (*Eichhornia crassipes* (Mart.) Solms) plants. *Aquat. Bot.* 37, 355–365.
- Ripley, B.S., Muller, E., Behenna, M., Whittington-Jones, G.M., Hill, M.P., 2006. Biomass and photosynthetic productivity of water hyacinth (*Eichhornia crassipes*) as affected by nutrient supply and mirid (*Eccritotarsus catarinensis*) biocontrol. *Biol. Control* 39, 392–400.
- Room, P.M., Thomas, P.A., 1985. Nitrogen and establishment of a beetle for biological control of the floating weed salvinia in Papua New Guinea. *J. Appl. Ecol.* 22, 139–156.
- Silveira-Guido, A., Perkins, D.B., 1975. Biology and host specificity of *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae), a potential biological control agent for water hyacinth. *Environ. Entomol.* 4, 400–404.
- Soti, P.G., Volin, J.C., 2010. Does water hyacinth (*Eichhornia crassipes*) compensate for simulated defoliation? Implications for effective biocontrol. *Biol. Control* 54, 35–40.
- Stanley, J.N., Julien, M.H., Center, T.D., 2007. Performance and impact of the biological control agent *Xubida infusella* (Lepidoptera: Pyralidae) on the target weed *Eichhornia crassipes* (waterhyacinth) and on a non-target plant, *Pontederia cordata* (pickerelweed) in two nutrient regimes. *Biol. Control* 40, 298–305.
- StatSoft Inc., Saranya, V., 2001. Statistica 6.0 Data Analysis Software System. StatSoft Inc., Tulsa, Oklahoma.
- Taylor, M.F.J., 1984. The dependence of development and fecundity of *Samea multiplicalis* on early larval nitrogen intake. *J. Insect Physiol.* 30, 779–785.
- Taylor, M.F.J., 1989. Compensation for variable dietary nitrogen by larvae of the salvinia moth. *Funct. Ecol.* 3, 407–416.
- Van Hezewijk, B.H., De Clerck-Floate, R.A., Moyer, J.R., 2008. Effect of nitrogen on the preference and performance of a biological control agent for an invasive plant. *Biol. Control* 46, 332–340.
- Vieira, M.deF., dos Santos, A.C., 2003. Life cycle of *Cornops aquaticum* (Brüner 1906) (Orthoptera: Acrididae, Leptysminae) and aspects of its food behaviour at Central Amazonia. *Acta Amazonica* 33, 711–714.
- Wheeler, G.S., 2001. Host plant quality factors that influence the growth and development of *Oxyops vitiosa*, a biological control agent of *Melaleuca quinquenervia*. *Biol. Control* 22, 256–264.
- Wheeler, G.S., 2003. Minimal increase in larval performance of the biological control agent *Oxyops vitiosa* when fed *Melaleuca quinquenervia* leaves of different nitrogen levels. *Biol. Control* 26, 109–116.
- White, T.C.R., 1976. Weather, food and plagues of locusts. *Oecologia* 22, 119–134.
- Xhong-xian, L., Xiao-ping, Y., Heong, K., Cui, H., 2007. Effect of nitrogen fertilizer on herbivores and its stimulation to major insect pests in rice. *Rice Sci.* 14, 56–66.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth ed. Prentice Hall, Upper Saddle River, New Jersey.