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

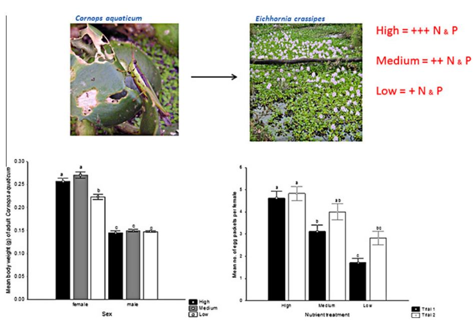
Angela Bownes[a,b,*], Martin P. Hill[b], Marcus J. Byrne[c]

[a] Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI), Private Bag X6006, Hilton 3245, South Africa
[b] Department of Zoology and Entomology, P.O. Box 94, Rhodes University, Grahamstown 6140, South Africa
[c] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag X3, Wits, Johannesburg 2050, South Africa

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.

* Corresponding author. Address: ARC-PPRI Weeds Division, Private Bag X6006, Hilton 3245, South Africa. Fax: +27 (0) 33 355 9423.
E-mail addresses: BownesA@arc.agric.za (A. Bownes), M.P.Hill@ru.ac.za (M.P. Hill), Marcus.Byrne@wits.ac.za (M.J. Byrne).

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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 (Kytö 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 already 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 *Eccritotarsus catarinensis* Carvalho (Hemptera: 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* Brüner (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