Proc. VII. Int. Symp. Biol. Contr. Weeds, 6-11 March 1988, Rome, Italy.
Delfosse, E.S. (ed.). Ist. Sper. Patol. Veg. (MAF), pp. 395 - 99 (1989).

Ovipositional and Feeding Habits in Cactophagous Pyralids: Predictions for Biological Control of Cactus Weeds in Southern Africa

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Abstract

The largest taxon of insect herbivores associated with cacti is the lepidopteran family Pyralidae in which four ovipositional habits are recognised; the eggs are laid either singly or clustered and are laid either on the thorns or on the surface of the cladodes. Most species lay single eggs on the thorns of the host. Four cactophagous pyralids have been introduced into South Africa for biological control of cactus weeds but only two have become established following mass releases. The two species that failed to established, *Tucumania tapiacola* and *Nanaia* sp., both lay single eggs on the cactus thorns and, in South Africa, over 80% of these eggs were destroyed by predators, mostly ants, or climatic extremes. *Cactoblastis cactorum* glues its eggs one on top of the other in "sticks" attached to the cactus thorns and it suffered levels of egg mortality similar to those of *T. tapiacola* and *Nanaia* sp. Mortality was lower for *Mimorista pulchellalis* eggs which are flat and laid on the cuticular surface of the cactus cladode. Mortality of the gregarious first-instar larvae of *C. cactorum* was lower than that of *T. tapiacola* and *Nanaia* sp., enabling *C. cactorum* to overcome the deleterious effects of low egg survival. The relatively impenetrable epidermal layers and the large amounts of gum that exude at the sites of insect damage are characteristic of the large tree-like *Opuntia* cacti and protect them from endophagous insect herbivores. The gregarious habit enables *C. cactorum* to usually breach these defences. The vulnerability of the eggs and first-instar larvae of pyralid species that lay single eggs on the thorns of their host plants precludes them from southern Africa although they constitute the largest group of potential biological control agents for cactus weeds.

Introduction

Several *Opuntia* species (Cactaceae), notably *O. aurantiaca* Lindley and *O. ficus-indica* (L.) Miller, remain problem weeds of varying importance in southern Africa in spite of protracted attempts at biological, mechanical and chemical control (Zimmermann and Moran 1982). Additional cactophagous insect herbivores are continually being sought to enhance biological control of these cactus weeds.

Approximately 160 monophagous and oligophagous insect species have been collected from the Cactaceae (Mann 1969, Zimmermann 1984). Besides being the dominant element of the cactus herbivore fauna, the larvae of the cactophagous pyralids are all borers and cause extensive damage on the plants by tunnelling into and through the cladodes (Moran 1980). This primary feeding damage is usually compounded by secondary microbial rot. The pyralids are therefore potentially excellent biological control agents and have been favoured for introduction against the cactus weeds in South Africa.

So far four pyralid species, *Cactoblastis cactorum* (Berg), *Mimorista pulchellalis* (Dyar), *Tucumania tapiacola* Dyar and an undescribed species of *Nanaia*, have been released in South Africa. Only the first two species have become established, the last two failing to produce viable populations following release.

Studies were conducted to quantify the adverse factors acting against the immature stages, particularly the eggs and first-instar larvae, of *T. tapiacola*, *M. pulchellalis* and *Nanaia* sp., in South Africa. The results are presented and a comparison is made of the survival of these three species with that of *C. cactorum*, which was studied by Robertson (1985). The most vulnerable stages in the life cycles of *T. tapiacola* and *Nanaia* sp. were identified and the implications of these findings for the future use of cactophagous pyralids in biological control of cactus weeds in southern Africa are discussed.

Methods and Materials

The survival of eggs nd first-instar larvae of *T. tapiacola*, *M. pulchellalis* and *Nanaia* sp. was measured on *O. aurantiaca* at Thursford Farm (33°12'S 26°22'E), where Robertson (1985) studied *C. cactorum*, Andries Vosloo Nature Reserve (33°08'S 26°41'E) and Uitenhage (33°40'S 25°28'E) in the East Cape Province of South Africa. For each moth species eggs were obtained from laboratory colonies and then transferred to the experimental sites as follows. Single pairs of male and female adult moths were placed in perspex plexiglass cages that measured 30 x 30 x 30 cm and had nylon gauze lids. The cages were furnished with a wad of cotton wool soaked in 5% sucrose as food and with either a potted *O. aurantiaca* plant or loose cladodes which provided an oviposition substrate for the female moths. The plants or cladodes were replaced in the cages daily. Eggs in excess of two to three per cladode were removed to achieve realistic densities of eggs on the plants and cladodes.

The potted plants with eggs were buried so that the surface of the soil in the pots was flush with that of the surrounding soil. Alternatively, thorns with eggs were removed from the cladodes and pushed into the areoles of plants growing in the field to simulate eggs that had been laid naturally. The cladodes with eggs of *M. pulchellalis* were placed among the cladodes of plants growing in the field.

The fate of the eggs and newly-hatched larvae was followed through daily observations. The numbers of first-instar larvae on the plants were increased by placing larvae that had hatched in the insectary onto plants in the field. Predators seen removing or feeding on the eggs and larvae were collected for identification.

Results and Discussion

T. tapiacola and *Nanaia* sp. both lay single eggs on the thorns of the host plant while *M. pulchellalis* lays flat single eggs closely pressed against the cuticle of the plant epidermis. *C. cactorum* lays long "sticks" with a mean of 54 (range = 4 - 111) eggs placed one on top of the other and with the basal egg attached to the tip of a thorn (Robertson 1987). Approximately 5% of the eggs laid by mated females were infertile (Hoffmann 1982, Robertson 1985).

Various mortality factors affected survival of the eggs in South Africa, including: predation by several ant species, a lygaeid bug and a predatory mite; parasitism by a Trichogrammatoidea species; the inclement affects of climatic extremes, particularly heavy rainfall (Hoffmann 1982, Robertson 1985). Although the damage caused by predators could be distinguished from that of parasitoids, most eggs simply disappeared from the plants and the mortality factor responsible could not be identified. In the presentation of the results no attempt is made to resolve the relative contribution of each mortality factor and survival of the eggs is presented as the percentage of eggs that hatched.

The combined mortality suffered by the eggs and first-instar larvae on the surface of the host plant was higher in *T. tapiacola* and *Nanaia* sp. than in *C. cactorum* and *M. pulchellalis*. The difference can be correlated with the ovipositional strategies of the female moths and with the behaviour of the first-instar larvae.

Survival was lowest for eggs that were laid on cactus thorns and was highest in *M. pulchellalis* eggs that were laid on the plant surface (Table 1). Survival of the eggs was generally higher (not in the case of *Nanaia* sp.) in the winter months than in summer. This may be attributed to lower levels of activity of predators in winter, an affect that was partially offset by longer exposure of the eggs to predators due to their longer incubation period (Hoffmann 1982). The impact of thunderstorms, which only occurred during the summer months in the study areas, also accounted in part for the greater mortality of eggs in summer (Hoffmann 1982, Robertson 1985).

Table 1. Percent survival, from oviposition to hatch, of the eggs of four cactophagous pyralid moths in South Africa during winter (April - July) and summer (November - February). The initial number of eggs from which the percentages were calculated is given in parentheses. Data for *C. cactorum* from Robertson (1985).

Moth species	Oviposition habit	Summer	Winter
Tucumania tapiacola Dyar	Single on thorns	14.0% (1481)	20.3% (1096)
Nanaia sp.	Single on thorns	20.4% (147)	18.6 (118)
Mimorista pulchellalis (Dyar)	Single on cuticle	Approx. 45%[1]	-
Cactoblastis cactorum (Berg)	'Sticks' on thorns		
	- on *O. ficus-indica* (L.) Miller	18.1% (7463)	32.1% (5852)
	- on *O. aurantiaca* Lindley	13.1 (2359)	18.8% (2357)

[1] Original data lost.

The solitary-feeding pyralid species were unable to establish themselves in the mature cladodes of the tree-like prickly pear *O. ficus-indica* (Table 2) because most of the first-instar larvae could not penetrate the tough epidermis of these plants and the few solitary larvae that did were always repelled by the large amounts of gum secreted by *O. ficus-indica* at the site of the insect damage.

Even on *O. aurantiaca*, where gum plays a minor role in the defence of the plant (Hoffmann 1976), the survival of the newly-hatched first-instar larvae was much lower in the solitary-feeding species than in the gregarious *C. cactorum* (Table 2). This may be attributed to the length of time taken by the larvae to penetrate the cacti and thus to the period that the larvae were exposed to predators and adverse environmental factors on the outside of the plant. Although no measurements have been made to specifically test this hypothesis, the solitary-feeding species generally took longer to get into the plant (up to 48 hours in the case of *T. tapiacola*) while *C. cactorum* usually achieved this in under two hours. The better survival among first-instar larvae of *Nanaia* sp. and *M. pulchellalis* compared to *T. tapiacola* may also be related to the time taken to penetrate the plant. Both *Nanaia* sp. and *M. pulchellalis* fed, initially at least, in the young terminal cladodes that were relatively easy to penetrate. The first-instar larvae of *T. tapiacola* on the other hand usually moved to the base of the plant after hatching and took longer to penetrate the old, tough basal cladodes.

The fecundity of *T. tapiacola* and *Nanaia* sp. averaged 309 and 175 eggs per female respectively. Given this fecundity, a population of *T. tapiacola* would be able to persist with only 0.7% survival of the progeny from each female and *Nanaia* sp. would persist with only 1.1% survival. In *T. tapiacola* 2.9% of the eggs survived to become first-instar larvae that penetrated the host plant while in *Nanaia* sp. there was 10.1% survival. Although low, these levels of survival alone would not account for the failure of populations of either species to persist in South Africa. However, the mortality of the egg and first-instar larval stages contributed most to the low survival of *T. tapiacola* and *Nanaia* sp. and coupled with the additional mortality that inevitably affected the older larvae, pupae and adults (Hoffmann 1981, 1988) the populations of *T. tapiacola* and *Nanaia* sp. were unable to survive and become established.

The findings suggest that pyralid species that lay single eggs on the thorns of the host and have solitary-feeding larvae will not survive on cacti in South Africa and this has important consequences for the selection of potential biological control agents. Most of the cactophagous pyralids are of this type (Table 3) and they thus constitute the largest group of potential biological control agents for cactus weeds in South Africa. However, our experience with these species indicates that none will survive in South Africa and the choice of agents that are available for biological control of *O. aurantiaca* is markedly curtailed.

Table 2. Percent survival between eclosion and successful penetration of the host by first-instar larvae of three cactophagous pyralids in South Africa during summer (November - February) and winter (April - July). The initial number of larvae on the plants is shown in parentheses. Data for *Cactoblastis cactorum* from Robertson (1985).

Moth species	*Opuntia* host plant	Summer	Winter
Tucumania tapiacola	*O. ficus-indica* (L.) Miller	0.0 (350)	-
Dyar	*O. aurantiaca* Lindley	21.0% (160)	-
Nanaia sp.	*O. ficus-indica*	0.0% (110)	-
	O. aurantiaca	49.3% (148)	-
Mimorista pulchellalis	*O. ficus-indica*	0.0% (130)	-
(Dyar)	*O. aurantiaca*	Approx. 40%[1]	-
Cactoblastis cactorum	*O. ficus-indica*	71.2% (3146)	69.0 (2486)
(Berg)	*O. aurantiaca*	75.3% (3551)	72.3% (889)

[1] Original data lost.

Table 3. The genera, with number of species in parentheses, of cactophagous Pyralidae classified according to ovipositional strategies. The list includes genera for which the oviposition behaviour is known or can reasonably be inferred from larval behaviour.

Oviposition site	Eggs in clusters	Single eggs
Thorns	Phycitinae:	Phycitinae:
	Cactoblastis (4)	*Alberada* (3)[1]
	Cactobrosis (5)	*Amalafrida* (1)
	Melitara (4)	*Cahela* (1)
	Olycella (3)	*Eremberga* (3)[2]
		Nanaia (3)
		Olyca (1)[2]
		Ozamia (5)
		Rumatha (3)[2]
		Salambona (1)[2]
		Sigelgaita (4)
		Tucumania (1)
		Yosemitia (4)
		Pyralinae:
		Beebea (1)[2]
Cuticle of epidermis	Pyraustinae:	Pyraustinae:
	Megastes (1)	*Mimorista* (3)
		Noctuelia (1)[2]

[1] Sometimes laid in clusters of up to five eggs.
[2] Oviposition strategy not verified but inferred from larval habits.

Although biological control of weeds has traditionally been an empirical discipline dependent largely on trial and error (van Lenteren 1980, Myers 1985), there is a trend towards developing a better predictive theoretical basis for the selection of potential biological control agents (e.g., Lawton 1985). Our experiences with cactophagous pyralids in South Africa have allowed us to develop a predictive hypothesis, based on behavioural attributes of the insect species, that would preclude some pyralid species as biological control agents of cacti in South Africa. The study emphasises the value and importance of monitoring in detail all newly introduced biological control agents, even when they fail.

Acknowledgments

Our thanks to Drs H.G. Robertson and J.R. Hosking for their comments on a draft of the script.

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