Egg Predation by Ants as a Partial Explanation of the Difference in Performance of *Cactoblastis cactorum* on Cactus Weeds in South Africa and Australia

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Abstract

The mediocre performance of *Cactoblastis cactorum* in controlling *Opuntia ficus-indica* and *O. aurantiaca* in South Africa has been attributed mainly to incompatibility with these host plants. Mortality is high during larval penetration of the plants and larvae are unable to destroy woody cladodes. Life tables derived from a study of *C. cactorum* at a site near Grahamstown demonstrate the important role of egg predation by ants in reducing the effectiveness of *C. cactorum*. The consequence of this predation pre-empting density-dependent mortality in the larval stage is discussed. Available evidence suggests that egg predation is not as high in Australia as in South Africa. The greater impact of ants in South Africa partly explains the difference in performance of *C. cactorum* compared with that in Australia.

La Prédation des Oeufs par les Fourmis Explique, en Partie, les Différences Observées dans la Performance de *Cactoblastis cactorum* Comme Agent Biologique Contre les Plantes Nuisibles Cactées en Afrique du Sud et en Australie

La performance médiocre de *Cactoblastis cactorum* dans la lutte contre *Opuntia ficus-indica* et *O. aurantiaca* en Afrique du Sud a été attribuée principalement à l'incompatibilité qui existe entre l'insecte et ces plantes hôtes. Le taux de mortalité est élevé pendant la pénétration des larves dans les plantes, et les larves sont généralement incapables de détruire les cladodes ligneux. Les tables de survie tirées d'une étude sur *C. cactorum* en un site près de Grahamstown montrent que la prédation des œufs par les fourmis réduit considérablement l'efficacité de *C. cactorum*. L'auteur traite des répercussions de la prédation qui remplace les causes de mortalité liées à la densité au cours de l'étape larvaire. Les espèces de fourmis qui infestent *C. cactorum* sont plus nombreuses en Afrique du Sud qu'en Australie, tandis que la diversité des autres ennemis naturels est similaire dans les deux pays. La prédation par les fourmis, qui est plus important en Afrique du Sud, explique, dans une certaine mesure, les différences dans l'efficacité de *C. cactorum* constatées dans les deux pays.

Introduction

The spectacular success in Australia of *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) in controlling the shrub pears, *Opuntia inermis* (DC.) (Cactaceae) and *O. stricta* (Haworth) Haworth, was not repeated when it was introduced to South Africa against the tree pear, *O. ficus-indica* (L.) Miller. This has been attributed to *O. ficus-indica* being more resistant to attack because it has a high proportion of woody cladodes, which *C. cactorum* larvae are usually unable to destroy (Petley 1948; Monro 1975; Annecke and Moran 1978). *C. cactorum* also feeds on the narrow-jointed pear *O. aurantiaca* Lindley which is a weed in South Africa and Australia. The woody basal cladodes of this species are also resistant to *C. cactorum* attack and larvae rarely kill
entire plants (Dodd 1940; Pettey 1948; Moran and Annecke 1979). Woody cladodes not only prevent the complete destruction of *O. ficus-indica* and *O. aurantiaca* plants but also reduce the survival of larvae feeding in them (Pettey 1948).

The results presented below are based on a study at one site in South Africa in which oviposition, detailed life tables and effectiveness of *C. cactorum* as a biological control agent were compared for *C. cactorum* populations on *O. ficus-indica* and *O. aurantiaca*. Factors other than host plant resistance have reduced population levels of *C. cactorum* at this site, and one of the most important of these was predation of eggs by ants. The role of egg predation by ants in reducing the effectiveness of *C. cactorum* is discussed and compared in South Africa and Australia from these results and from published records.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>South Africa on <em>O. ficus-indica</em></th>
<th>Australia on <em>O. inermis</em> DC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>This study</td>
<td>Pettey (1948)</td>
</tr>
<tr>
<td>% egg mortality</td>
<td>74</td>
<td>—</td>
</tr>
<tr>
<td>% penetration mortality¹</td>
<td>19</td>
<td>—</td>
</tr>
<tr>
<td>% total larval mortality</td>
<td>54</td>
<td>—</td>
</tr>
<tr>
<td>% pupal parasitism</td>
<td>5</td>
<td>16</td>
</tr>
<tr>
<td>% other pupal mortality</td>
<td>35</td>
<td>35</td>
</tr>
<tr>
<td>% adult mortality — summer</td>
<td>46</td>
<td>—</td>
</tr>
<tr>
<td>% adult mortality — winter</td>
<td>84</td>
<td>—</td>
</tr>
<tr>
<td>Mean fecundity/female</td>
<td>(175)²</td>
<td>126</td>
</tr>
</tbody>
</table>

¹ Only includes mortality of whole colonies and not mortality within colonies.
² This value is higher than the other two because it does not include females that did not lay eggs, and was determined from tests undertaken in the laboratory, under optimal temperature conditions.

**Methods**

All field work was undertaken on a farm 19 km NW of Grahamstown. Seven adjacent 50 × 50 m quadrats were marked and all *O. ficus-indica* plants (*n* = 194) and *O. aurantiaca* clumps (*n* = 1316) contained in the quadrats were individually numbered. *O. aurantiaca* clumps consist of a cluster of intermingled plants of different sizes which for convenience are referred to as plants. To determine egg mortality, all *O. ficus-indica* plants and a sample of *O. aurantiaca* plants were searched almost daily for eggstics during the summer (October to December) and winter (February to May) egg-laying periods. Each eggstic was numbered, the number of eggs was counted, and egg mortality was checked on each subsequent day.

**Results and Discussion**

A comparison of penetration mortality, total larval mortality, and fecundity, which are all host plant-related factors, suggests that in *C. cactorum*, they are similar on *O. ficus-indica* in South Africa and *O. inermis* in Australia (Table 1): (1) penetration mortality was only 2–3% higher on *O. ficus-indica*; (2) total larval mortality on *O. ficus-indica* was within the range of 40–60% cited by Dodd (1940) for *O. inermis*;
and (3) average fecundity/female, based on Pettey’s (1948) and Dodd’s (1940) figures, was 7% lower on *O. ficus-indica*.

The reason why the greater host plant resistance of *O. ficus-indica* is not markedly reflected in these results is because, firstly, females oviposit mostly on terminal, succulent cladodes (Robertson, unpubl. data) and secondly, succulent cladodes are usually sufficient for the food requirements of larvae. Except on small plants, larvae on plants at the study site were rarely at densities where they were forced to feed on the woody cladodes.

Drawing conclusions from the above results has risks as parameters were measured and data were interpreted in different ways. However, the data indicates that difference in performance of *C. cactorum* in South Africa and Australia cannot be entirely linked to differences in the resistance of the two host plants to attack. Table 1 shows that other factors might also be responsible. Dodd (1940) does not give values for egg mortality of *C. cactorum* in Australia but results in Table 1 show that in the study area in South Africa it was very high. Pupal parasitism, based on the extensive results of Pettey (1948) and Dodd (1940), is only about 3% higher in South Africa, but mortality of pupae from other factors is 10% higher than in Australia. Adult female mortality (= pre-oviposition egg mortality) has not been measured in Australia, but in South Africa was deduced indirectly in this study as 46% in the summer 1981–82, and 84% in the winter 1982 generation. Low temperatures reduce fecundity and decrease survival of females (Pettey 1948) which probably accounts for the high mortality in the winter generation. In Australia, temperature also affects fecundity and adult mortality (Dodd 1940), but whether it does so to the same extent as in South Africa is not known.

The high mortality of *C. cactorum* eggs recorded in this study is mostly due to predation by at least eight species of ants. Recorded species are: *Crematogaster liengmei* Forel, *Pheidole* sp., *Tetramorium erectum* Emery, *T. bacchus* Forel, *Tetramorium* sp., *Monomorium albopilosum* Emery, *M. minutum* Mayr., and *Camponotus nivesetosus* Mayr. An unidentified mite and a lygaeid bug (*Nyisia* sp.; Hemiptera: Lygaeidae) were also recorded as predators of *C. cactorum* eggs, but in relation to ants their effect is of minor importance. In addition to egg predation, eggsticks were sometimes broken off, either partly or completely, by adjacent vegetation brushing against them or by hail, heavy rain and wind.

There are four main reasons why egg predation by ants has been an important mortality factor affecting the *C. cactorum* population in this study: (1) *Magnitude*. Egg predation, mainly by ants, caused 60 and 55% mortality of eggs laid on *O. ficus-indica* in the summer 1981–82 and winter 1982 generations, respectively. These values were considerably higher on *O. aurantiaca*, accounting for 77 and 78% mortality respectively in each generation (Fig. 1). Observations in four other generations at the same site confirm that high egg predation is a general phenomenon. (2) *Life stage attacked*. Predation before the larval stage can decrease the amount of weed destruction more than the same amount of predation after this stage, as predation directly affects the proportion of eggs laid that hatch. The importance of this factor depends on the extent of density-dependent larval mortality, but this was not great in this study. (3) *Density-dependence*. There is evidence that predation by ants of *C. cactorum* eggs is spatially density-dependent (Robertson, unpubl. data). This factor could increase the dampening of *C. cactorum* populations caused by egg predation, although other factors such as season and prevailing temperatures tend to obscure its effects. (4) *Ants are generalists*. *C. cactorum* eggs would form only a small fraction of the food consumed by each of the ant species that feed on them. Eggstick density would therefore have little effect
on ant population numbers and ants would respond directly to changes in eggstick densities between generations. In addition, ants are attracted onto *O. ficus-indica* and *O. aurantiaca* plants by extra-floral nectar production and this might further increase the speed of their response to eggstick presence.

Predation of *C. cactorum* eggs by ants appears to be widespread in South Africa, although in some areas other factors might be more important in limiting population numbers. I have observed extensive egg predation in a valley-bushveld site near Uitenhage and in Fish River scrub vegetation near Fort Brown. Pettie (1948) found that ants attacked all stages of *C. cactorum* except the adult and considered that they

![Diagram](image)

**Fig. 1.** Mortality of *Cactoblastis cactorum* (Berg) eggs on *Opuntia ficus-indica* (L.) Miller and *O. aurantiaca* Lindley in the summer 1981–82 and winter 1982 generations at a site near Grahamstown.

had probably caused more mortality of *C. cactorum* in South Africa than any other predators. He recorded that several species of small ants removed eggsticks from the paper quills in which they had been placed for distribution purposes. He reports on an experiment in which predation of eggsticks in paper quills was measured at seven sites. At five of these sites, only 2–7% of the eggsticks were removed from the quills, whereas at the other two sites ants caused 30 and 59% mortality. These results are under-estimates for two main reasons. Firstly, eggsticks of unknown age were used. Thus, during the experiment, eggsticks were not exposed to predation for their entire development period. Secondly, these tests were conducted in May (winter). Ant
predation of eggs is strongly influenced by season and prevailing temperatures (Robertson, unpubl. data). For instance, at the study site near Grahamstown, predation was at its peak during March, dropped sharply during April, and by May was at a low level. Of the eggs remaining on O. ficus-indica plants at the beginning of May, only 16% were eventually destroyed by ants.

Ant predation of C. cactorum eggs also occurs in Australia, but available evidence suggests that it is not as severe as in South Africa. Dodd (1940) records egg predation by Iridomyrmex ants but regarded this as being unusual. He mentions that small ant species, such as Crematogaster, may eat some of the eggs in a stick but does not detail the extent of this predation. Compared with Australia, there are more ant species recorded attacking C. cactorum in all its stages in South Africa while the diversity of other natural enemies is similar.

During a study of eggstick clumping on O. inermis in Australia, Monro (1967) located 1178 eggsticks at eight different sites, but makes no mention of egg predation affecting his estimates of eggstick densities. Later (Monro 1975), he mentions that in the southern part of the range of C. cactorum in Australia, there is 'an almost classic two species interaction with little interference from predators or competitors'. White (1981) determined eggstick densities on O. inermis plants, but also does not mention egg predation. In the study undertaken near Grahamstown, 49% of eggsticks on O. ficus-indica were completely destroyed by ants at the end of the summer and winter generations, many of which had completely disappeared. Eggstick densities would therefore have been very under-estimated if the same methods as Monro (1967) and White (1981) had been used.

Hoffmann (1981) recorded 80% mortality of Tucumania tapiacola Dyar (Lepidoptera: Pyralidae) eggs in South Africa caused mostly by ants. The reason this moth was successfully established on O. aurantiaca in Australia (Dodd 1940) but not South Africa (Hoffmann 1982) is possibly related to the excessive egg predation by ants occurring in South Africa.

There is a need for clarification on the extent of predation by ants of C. cactorum eggs in Australia. Available evidence, however, suggests that whereas in Australia, population numbers of C. cactorum are limited by density-dependent larval mortality, in South Africa, larval densities are often kept at low levels by other mortality factors — especially ant predation in the egg stage. Even if population levels of C. cactorum were much higher, its performance on O. ficus-indica and O. aurantiaca would still not match that on O. inermis and O. stricta in Australia because it is inefficient at destroying woody cladodes. Nevertheless, C. cactorum can destroy O. ficus-indica plants with less than 15 cladodes (Zimmermann and Malan 1981) and also reduces the size and vigour of O. aurantiaca and large O. ficus-indica plants. Egg predation has lowered the extent of this damage.

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References


