

THE BIOLOGICAL CONTROL OF *HAKEA SERICEA* SCHRADER
BY THE *HAKEA* SEED-MOTH, *CARPOSINA AUTOLOGA* MEYRICK,
IN SOUTH AFRICA

THESIS

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ANTHONY JOHN GORDON

Department of Zoology and Entomology
Rhodes University
Grahamstown, South Africa

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ABSTRACT

Hakea sericea Schrader was introduced to South Africa from Australia and has become a major problem in nearly all the coastal mountain ranges of the Cape Province. The hakea seed-moth, *Carposina autologa* Meyrick was released in South Africa for the biological control of *H. sericea*. The impact of the moth on the canopy-stored seeds of *H. sericea* was evaluated at two study sites in the south-western Cape over three years. The moth has reduced the accumulated seeds at the two study sites by 59.4% and 42.6%, respectively. The moth has shown a surprising ability to disperse and establish new colonies at low population levels.

Factors contributing to the slow colonization of *C. autologa* in South Africa was investigated. The moths appear to be unable to distinguish between healthy and previously attacked fruits; 42.5% of the eggs were laid on attacked fruits. Only 13.1% of the healthy fruits with eggs yielded mature larvae. The high pre-penetration mortality found in the present study is similar to that found in Australia.

The effect of the indigenous fungus, *Colletotrichum gloeosporioides* (Penz.) Sacc., on both *H. sericea* and *C. autologa* was investigated. *H. sericea* trees and branches that die as a result of fungus cause the accumulated fruits on the affected trees or branches to dehisce. This seed loss occurs at a crucial stage during *C. autologa* larval development. Only 42.1% and 33.0% of the trees were found to be healthy at the two study sites, respectively.

One seed crop will always be available for regeneration, since recruitment is linked to fires, and wild-fires occur

at a stage when the latest seed crop has escaped attack by *C. autologa*. *C. autologa* was released at six sites in the south-western Cape by attaching egg-bearing follicles to healthy fruits in the field. Three release sites were evaluated the year following release to determine whether the moth established or not.

The role of *C. autologa* in the *H. sericea* biological control programme is discussed. Although seed destruction by *C. autologa* is not severe, it is expected to contribute to the control of *H. sericea*.

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PREFACE

Hakea sericea Schrader was introduced from Australia during the 1930's and has become a major problem in nearly all the coastal mountain ranges of the Cape Province where it often forms dense, impenetrable thickets and poses a serious threat to the floristically rich and unique mountain "fynbos" (macchia).

In order to reduce the number of seeds released after fires, two seed-feeding insects were introduced from Australia. The weevil, *Erytenna consputa*, which destroys the immature fruits of *H. sericea* and the seed-moth, *Carposina autologa*, which attacks mature seeds in fruits escaping *E. consputa*.

The effect of *C. autologa* on *H. sericea* was evaluated shortly after release in 1982. Infestation levels were found to be low and population levels decreased over the study period. This led to the suspension of the *C. autologa* project in 1984. However, in 1987 it was discovered that many of the fruits at the release sites contained *C. autologa* emergence holes indicating a recovery in the moth population. It was therefore decided to re-evaluate *C. autologa* as a biological control agent.

The main aims of this thesis were to evaluate the impact of *C. autologa* on the canopy-stored seeds of *H. sericea* and to investigate those factors that could have contributed to the slow colonization of *C. autologa*.

Chapter 1 is an introduction to the *H. sericea* problem and factors thought to have contributed to the success of *H. sericea* as an invader in South Africa. The initial

introduction and evaluation of the efficacy of *C. autologa* is also discussed.

Chapter 2 concerns the evaluation of the impact of *C. autologa* on the canopy-stored seeds of *H. sericea*. This includes the determination of the level of infestation, and total seed destruction achieved by *C. autologa*. The dispersal ability of *C. autologa* is also examined.

Factors that have contributed to the slow colonization of *C. autologa* in South Africa are investigated in Chapter 3. The effect of an indigenous fungus, *C. gloeosporioides*, on both *H. sericea* and *C. autologa* populations is investigated in Chapter 4.

Chapter 5 poses the question "Have insect-host plant relationships influenced estimation of the efficacy of *C. autologa*?". Chapter 6 concerns the evaluation of an alternative method of release and the redistribution of *C. autologa*.

Chapter 7 is an overview of the role of *C. autologa* in the *H. sericea* biocontrol programme.

CHAPTER 1

INTRODUCTION

Hakea sericea Schrader or silky hakea, is an erect single-stemmed, much-branched shrub which grows to a height of 2-5 metres. It was introduced to South Africa from Australia during the 1930's (Neser & Fugler, 1978). The earliest documented record of its occurrence in the south-western Cape was in 1858 when it was listed as one of the plants growing in the Botanical gardens in Cape Town (Shaughnessy, 1980).

Hakea sericea has become a major problem in nearly all the coastal mountain ranges of the Cape Province (Neser & Fugler, 1978) where it often forms dense, impenetrable thickets and poses a serious threat to the floristically rich and unique mountain fynbos. In 1983 almost 480000ha of mountain fynbos were affected by hakea infestations of varying degrees (Kluge & Richardson, 1983). *Hakea sericea* was rated as the sixth most important invasive vascular plant species in the fynbos biome (Macdonald & Jarman, 1984; Richardson *et al.*, 1992). Macdonald (1984), in his paper on the susceptibility of the fynbos biome to the invasion by alien plants, reports that hakea infestations cover between 12% and 20% of mountain fynbos.



Plate 1. A dense infestation of *Hakea sericea* invading indigenous mountain fynbos at Burnsleigh in the southern Cape.

Reasons for success

Factors thought to have contributed to the success of *H. sericea* as an invader in South Africa are its copious production of serotinous seeds, the high seed longevity in the canopy, and the efficient seed dispersal.

Copious seed production and serotinous habit. In dense, mature stands of *H. sericea*, seed densities up to 7500 seeds/m² have been reported (Kluge, 1983). Four to five meter tall trees may produce as many as 10 000 seeds (A.J. Gordon, unpublished data, 1989). A large seed crop is important in overcoming post-dispersal mortality and gives the plant an advantage in reaching and competing in as many germination sites as possible (Neser & Kluge, 1986).

In Australia, where *H. sericea* is relatively rare, its seeds are subject to attack by numerous insect species (Neser, 1968). In South Africa, however, before the introduction of biological control agents, there was virtually no pre-dispersal predation. Richardson *et al.* (1987) suggest that the success of *H. sericea* relative to other alien hakea species is largely due to its production of large numbers of viable seed. To demonstrate this, they compared the seed production of *H. sericea*, *Hakea gibbosa* (Sm.) Cav., *Hakea drupacea* (Gaertn.f.) Roemer & Schultes (= *Hakea suaveolens* R. Br.) and *Hakea salicifolia* (Vent.) B.L. Burtt. (syn. *H. saligna* Knight) in the south-western Cape. Of these the three first-mentioned are declared noxious weeds in South Africa and form dense thickets. However, it is only in the case of *H. sericea* that colonization of distant areas constitutes a major problem. They ascribe the limited areal expansion of *H. gibbosa* and *H. drupacea* populations to their



Plate 2. The abundance of canopy-stored fruits on an old H. sericea plant.

lower seed production.

The seeds produced annually are stored in the canopy and are only released after fire (pyriscence, *sensu* Lamont, 1991) or death of the plant. All the follicles open a few days after a fire, simultaneously releasing the seeds which germinate in autumn. Fires are an important feature of the fynbos vegetation and are necessary for species survival (van Wilgen, 1981a; van Wilgen & Richardson, 1985). Recruitment after fire would therefore depend not only on the most recent seed crop, but also on nearly all the seeds produced during the plant's lifetime.

High seed longevity in the canopy. The seeds of *H. sericea* remain viable for many years while they are still inside the healthy follicle (Neser, 1968). The fruit of *H. sericea* consists of a woody follicle comprising two dehiscent valves. Each valve contains one, black, winged seed. Each seed is 8mm long and 5mm wide and has a 15mm long and 10mm wide membranous wing. Richardson *et al.* (1987) found no significant difference between the viability of young and old canopy-stored seeds of *H. sericea* with the mean viability being 99%. In the absence of pre-dispersal predators, this large quantity of accumulated viable seed is available for simultaneous release.

Efficient seed dispersal. Although few plant species have seeds that are dispersed over greater distances than a few times the height of the parent tree (Harper, 1977), the winged seeds of *H. sericea* facilitate dispersal over several kilometers in some cases (Richardson *et al.*, 1987). These seeds then form the nucleus of new infestations. The importance of nascent foci in the spread of plant invasions have been elucidated by Moody and Mack (1988). There is

little evidence of active dispersal of *H. sericea* by human agency (Shaughnessy, 1980), birds or animals and therefore the widespread distribution is largely due to the winged seeds being dispersed over long distances by strong winds.

Present control strategies

The present control methods include both mechanical and biological control. Mechanical control is an extremely effective method of controlling *H. sericea* (Fenn, 1980), but the programme has suffered from a combination of high costs and budgetary constraints. This method involves felling adult plants and leaving them for 12-18 months to allow the canopy-stored seeds to be released and to germinate. Because the plants are felled, the seeds are released nearer the ground, and dispersal of the winged seeds is reduced. Once the seedlings emerge, the area is burnt (Kruger, 1977; Fugler, 1982). However, this technique leads to increased fire intensity which has a negative effect on the ecosystem (Richardson & van Wilgen, 1986; Breytenbach, 1986; 1989).

In order to reduce the number of seeds released after fires, two seed-feeding insects were introduced from Australia. The weevil, *Erytenna consputa* Pascoe (Curculionidae: Eriirhininae), which destroys the immature fruits of *H. sericea* and whose adults feed on buds, flowers and young fruits, was released in 1972 (Neser & Annecke, 1973). *E. consputa* was the first biological control agent successfully established against *H. sericea* in South Africa. At a study site in the south-western Cape, where 20 adults were released in 1975, fruit loss increased to 81%, of which 86% was due to *E. consputa* activity (Neser & Kluge, 1985).

However, *E. consputa* does not appear to be equally effective throughout the range of the weed and an evaluation study on its effectiveness is presently in progress.

The hakea seed-moth *Carposina autologa*

The hakea seed-moth, *Carposina autologa* Meyrick (Lepidoptera: Carposinidae), which attacks mature seeds in fruits escaping predation by *E. consputa* was expected to adequately supplement the weevil, and was introduced in 1970. The biology and phenology of *C. autologa* have been described by Naser (1968); it is univoltine with no diapause or quiescent phase, eggs being laid singly on the surface of mature fruits or between touching fruit in autumn. The eggs hatch a few weeks later and the larvae enter the fruit at a point along the suture on the axial surface of the fruit, one larva only developing per fruit. The larva feeds on one seed initially and attacks the other seed once the first has been consumed, both being needed to complete development. During the third instar the larva prepares an exit tunnel through the woody fruit, and alternates between feeding and excavating the tunnel. Mature larvae emerge from the tunnel, fall to the ground and pupate in the soil.

Various methods were used to release *C. autologa* in the field and included placing newly-hatched larvae onto fruits, inserting larvae directly into fruits or releasing late instar larvae and moths, the most successful method being to insert larvae into holes drilled in the fruits (Dennill, 1987a).

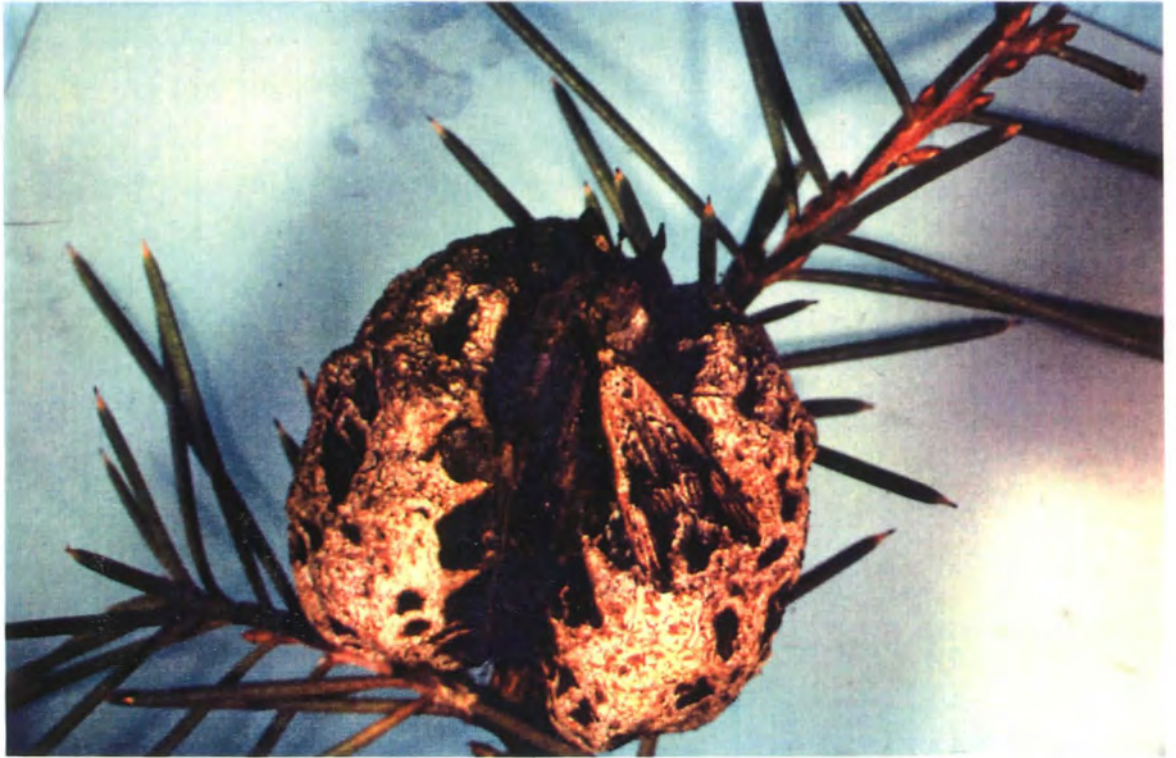


Plate 3. Hakea seed-moth Carposina autologa on a mature Hakea sericea fruit. Photo: Dr. S. Nesor.

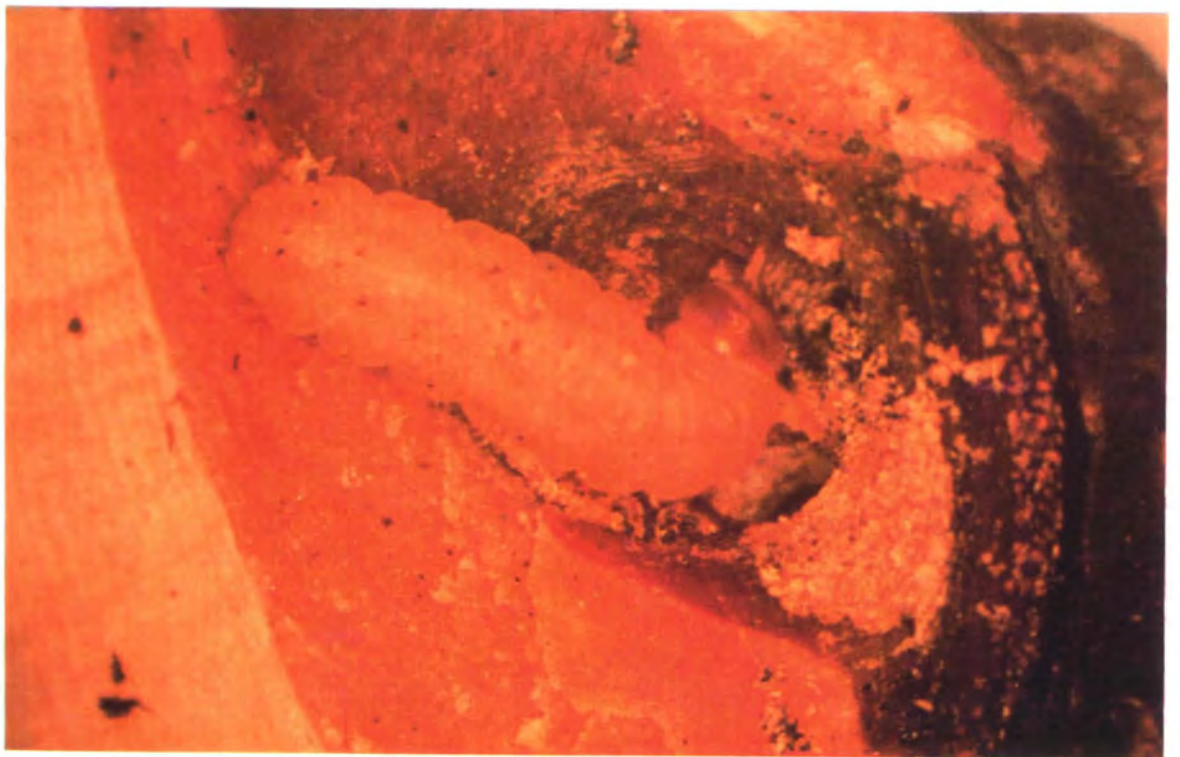


Plate 4. A full grown Carposina autologa larva with the entrance to the exit tunnel clearly visible to the right of the larva.

H. sericea fruits with *C. autologa* eggs were collected in Australia and air-freighted to South Africa. The fruits were surface-sterilized and kept in quarantine and inspected daily for hatching larvae. The hatched larvae were removed and placed individually onto a synthetic diet (Harley and Wilson, 1968) and allowed to feed for a week or two before being inserted into fruits in the field. A small hole (approximately 1mm in diameter) was drilled into a mature fruit through to the seed cavity using a portable dental drill. A larva was then placed onto the fruit and coaxed into the hole which was then sealed with wax. The larvae were allowed to develop and emerge naturally on the trees. Although this method proved to be the most successful it was extremely time consuming and labour intensive.

Despite difficulties with rearing and releasing this insect (Dennill 1987a; Dennill *et al.*, 1987) it was finally established at six sites in the south-western Cape (Table 1; Fig. 1), four of which, however, were subsequently felled or burnt. The effect of *C. autologa* on *H. sericea* was evaluated at two of these sites (Paradyskloof and Stellenbosch Mountain) shortly after release. Infestation levels were low and population levels decreased over the study period (Dennill *et al.*, 1987). One of the factors contributing to the decline of *C. autologa* populations was that trees were dying or dead because of attack by an indigenous fungal pathogen, *Colletotrichum gloeosporioides* (Penz.) Sacc., which caused die-back and death of *H. sericea* (Morris, 1982a; Dennill *et al.*, 1987). This led to the suspension of the project in 1984.

During a visit to Paradyskloof to collect *H. sericea* seeds in 1987, however, it was discovered that many of the fruits contained *C. autologa* emergence holes indicating a recovery

Table 1. Summary of releases of *C. autologa* in the south-western Cape. Prior to 1977 larvae were released onto fruits and after 1977 the larvae were inserted into fruits. * indicates releases of adults.

Release site	Date	No. of individuals released
Paradyskloof (33°59'S;18°53'E)	1977	498*
	1978	274
	1979	515
	1981	214
Knorhoek (34°06'S;18°57'E)	1981	574
Stellenbosch Mt. (33°57'S;18°54'E)	1980	1065
	1981	217
Wemmershoek (33°51'S;19°08'E)	1970	240
	1971	100
		100*
	1975	800
	1982	783
Coetzenburg (33°56'S;18°53'E)	1978	541
Goudini Spa (33°40'S;19°16'E)	1982	1004
Total		7005

in the moth population. It was therefore decided to re-evaluate *C. autologa* as a biological control agent.

The aims of this evaluative study were (1) to assess the impact of *C. autologa* on the canopy-stored seeds of *H. sericea* at the two remaining release sites (Paradyskloof

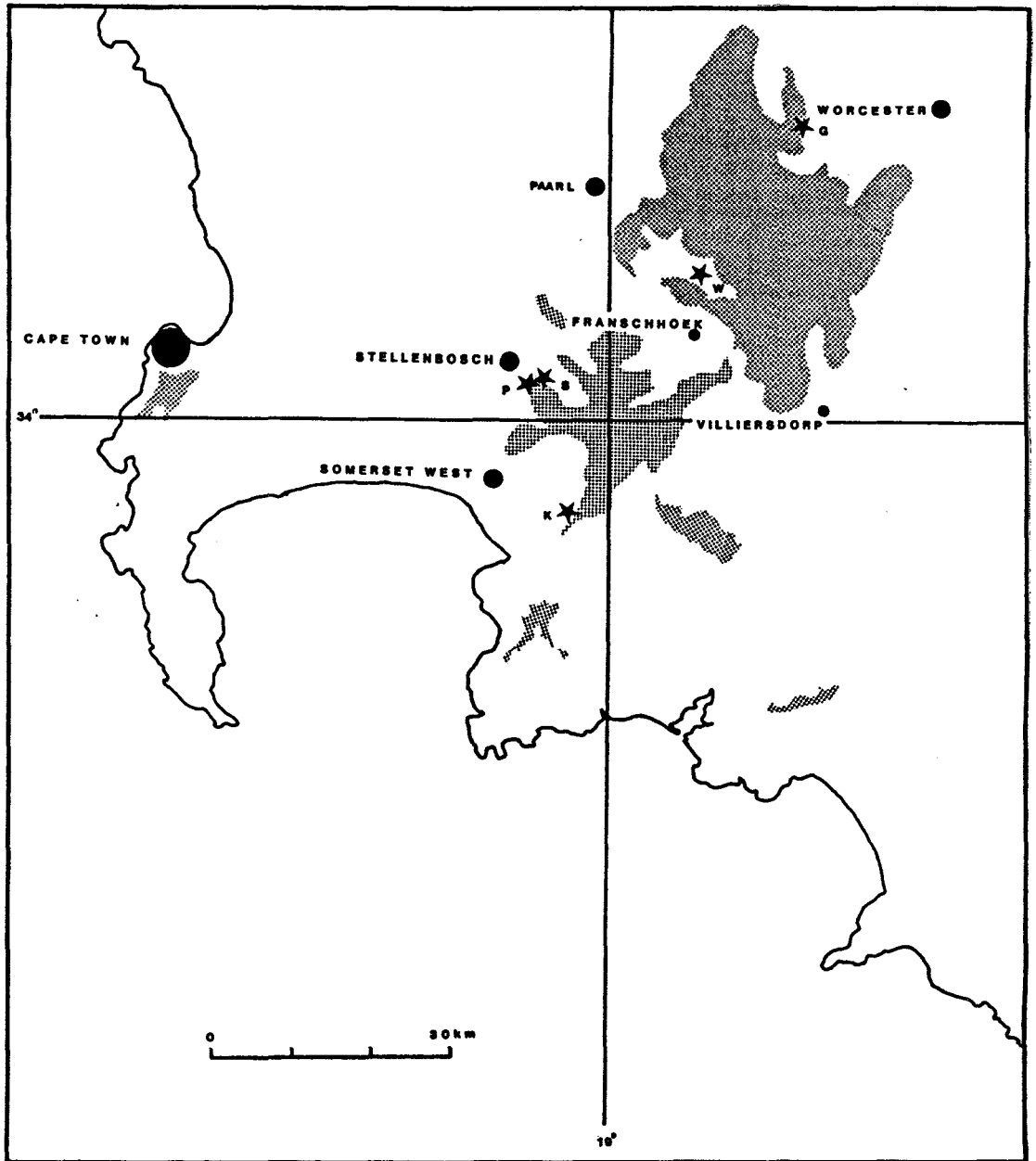


Fig. 1. The location of the *C. autologa* release sites (★) in the south-western Cape. G = Goudini Spa, W = Wemmershoek, S = Stellenbosch Mountain, P = Paradyskloof and K = Knorhoek. The shaded areas are the mountainous regions.

and Knorhoek) and to monitor moth population increases (Chapter 2), (2) to investigate mortality factors which could have contributed to the slow colonization of *C. autologa* (Chapter 3), (3) to evaluate the effect of the fungus *C. gloeosporioides* on both *C. autologa* populations and seed production of *H. sericea* (Chapter 4), (4) to investigate whether insect-host plant relationships influenced the estimation of the efficacy of *C. autologa* (Chapter 5), (5) to redistribute *C. autologa* throughout the South African range of the weed and to evaluate the method of release (Chapter 6), and (6) an overview of the biological control of *H. sericea* and the role of *C. autologa* in this programme (Chapter 7).

CHAPTER 2

The impact of the hakea seed-moth *Carposina autologa* (Carposinidae) on the canopy-stored seeds of the weed *Hakea* *sericea* (Proteaceae)

INTRODUCTION

The impact of *C. autologa* on *H. sericea* was first evaluated at Paradyskloof and Stellenbosch Mountain between 1982 and 1984. Although *C. autologa* had become established at these sites, infestation levels were low and population levels decreased over the sampling period (Dennill *et al.*, 1987). This led to the suspension of the *C. autologa* programme in 1984. During a visit to Paradyskloof to collect *H. sericea* seeds in 1987, however, it was discovered that many of the fruits contained emergence holes indicating an increase in moth activity. It was therefore decided to re-evaluate the efficacy of *C. autologa* and to investigate which factors were responsible for the initial, slow establishment. The aims of the study reported in this chapter were (1) to determine the level of infestation and population increase, (2) to assess the total seed destruction achieved by *C. autologa* on *H. sericea*, and (3) to examine the dispersal ability of the moth.

Data from this Chapter has been accepted for publication in Agriculture, Ecosystems and Environment.

METHODS

Study sites

The study sites were situated at Paradyskloof (33°59'S;18°53'E) and Knorhoek (34°06'S;18°57'E), the two remaining release sites where *C. autologa* populations survived. Paradyskloof is situated on the south-facing slopes of Stellenbosch Mountain and Knorhoek on the exposed north-facing slopes of the Hottentots Holland Mountains. The climate is mediterranean, humid-mesothermal (Csb) (Koppen, 1931) with average rainfall of 1700mm per annum, of which about 59% falls, between May and August. The density of the *H. sericea* trees was 0.45m² and 1.80m² at Paradyskloof and Knorhoek, respectively. The height of the trees varied between 1m and 6m at Paradyskloof and 1m and 3.5m at Knorhoek.

At both sites an area measuring 200m x 100m was marked out. Ten transects 20m apart were laid across these plots. At 10m intervals along each transect the nearest healthy *H. sericea* tree was selected and permanently tagged. In this way, 91 and 100 trees were selected at Paradyskloof and Knorhoek, respectively. Only healthy trees were selected as many of the trees were infested with the fungus, *Colletotrichum gloeosporioides* (Penz.) Sacc. (see Chapter 3), which causes die-back and death of *H. sericea* (Morris, 1982a).

Levels of infestation

Destructive sampling could not be used to determine the level of seed predation at the study sites due to the low *C. autologa* population levels. The only clear way was to count the emergence holes. All the fruits on the sample trees were counted and examined for *C. autologa* emergence holes annually from 1988 to 1990. In spite of the height of some trees (5-6 metres) and abundance of fruits, which made the examination of the fruits difficult, the entire tree was sampled to circumvent the problems of sub-sampling. As each season's fruits are retained on the trees all fruits with emergence holes were marked with a small dab of PVA paint to distinguish them in subsequent censuses. The paint used does not affect the behaviour of the moths. The annual increase in the number of attacked fruits was used as an indication of the population increase.

Counts were usually made during summer and not immediately after larval emergence from the fruits because (a) the larvae that pupate in the leaf litter or in the soil close to the surface would be trampled during sampling and (b) the fruits are wet during winter, making it difficult to detect fruits with emergence holes. In the first year of study the fruits sampled included newly-set fruits which would not have been available for egg-laying. The reason for this was that the present study commenced late in the season and it was difficult to distinguish between old and new fruits (see Chapter 4). Fruits that had dehisced as a result of fungal damage were recorded separately, as *C. autologa* moths do not oviposit on dehisced fruits (Neser, 1968).

Total seed destruction

Although counting emergence holes is a good measure of population increase, it is not an ideal measure of actual seed destruction, because (a) larvae might die within the fruits after having destroyed one or both seeds and (b) seeds are also lost when fruits dehisce as a result of infection by the fungus, *C. gloeosporioides*. Therefore, at the end of the study, all the fruits were removed from the sample trees in September 1990 (3989 and 2155 fruits from Paradyskloof and Knorhoek, respectively) for examination under a binocular microscope to determine the fate of the seeds. As some of these fruits contained *C. autologa* larvae, this figure was used as an indication of the population increase for 1991 (see Table 3).

Dispersal

The data obtained from the studies above were used to determine the dispersal of *C. autologa* throughout the 2ha grid site. The presence or absence of fresh emergence holes on the sampled trees indicated whether *C. autologa* was present or not. To obtain an indication of long-distance dispersal, *H. sericea* stands around some of the original release sites (Fig.1) were selected for sampling. Because of the scarcity of mature *H. sericea* infestations in the vicinity of the original release sites, only five suitable sites were sampled. At each site, 40 trees were randomly selected and felled. All the fruits on the trees were counted, noting the number with *C. autologa* emergence holes.

RESULTS AND DISCUSSION

Levels of infestation

The levels of infestation achieved by *C. autologa* at both Paradyskloof and Knorhoek were higher than initially expected. At Paradyskloof the percentage of attacked fruits was 5.2% in 1982 and 5.6% in 1983 whereas none of the fruits sampled contained fresh emergence holes in 1984 (Dennill et al., 1987) (Table 2). Four years later (1988), 36.7% of the fruits had emergence holes which is a noticeable increase when compared with infestation levels found by Dennill et al. (1987). Between 1988 and 1990 the mean number of attacked fruits increased to 51.7%. However, there was no further increase in 1991 (50.4%; Table 3). The

Table 2. *Carposina autologa* infestation levels on *H. sericea* trees at Paradyskloof in the south-western Cape, and the percentage of trees killed by the fungus, *C. gloeosporioides* from 1982-1984 (reproduced from Dennill et al., 1987).

Year	No. of fruits sampled	No. (%) fruits attacked	No. of trees sampled	% of trees diseased
1982	1406	73 (5.2)	41	7.0
1983	550	31 (5.6)	31	44.0
1984	162	0 (0.0)	9	88.4

numbers of fruit examined at each site in the different years are shown in Table 3.

At the Knorhoek site the initial population comprised 574 larvae inserted into fruits, as described above, in 1981 (Kluge & Naser, 1991). From this release 279 full grown larvae successfully emerged from the fruits the following year. In 1988, six years later, 13.8% of the fruits sampled had emergence holes and by 1991 the mean number of attacked fruits had increased to 36.8% (Table 3). The mean number of attacked fruits per tree increased steadily over the study period and there was a corresponding decrease in the mean number of healthy fruits per tree between 1988 and 1990 despite the annual increment of new fruits (Fig. 2). The

Table 3. *Carposina autologa* infestation levels on *H. sericea* at Paradyskloof and Knorhoek, 1988-1991.

Site	Year	No. of fruits sampled	Mean % fruits attacked (\pm SE)
Paradyskloof (n=91 trees)	1988	2583	36.7 (\pm 2.97)
	1989	2583	45.3 (\pm 3.13)
	1990	3070	51.7 (\pm 3.00)
	1991	3989	50.4* (\pm 2.83)
Knorhoek (n=100 trees)	1988	1772	13.8 (\pm 1.94)
	1989	1772	29.9 (\pm 2.43)
	1990	1907	36.8 (\pm 2.56)
	1991	2155	40.7* (\pm 2.50)

* includes fruits with larval *C. autologa*

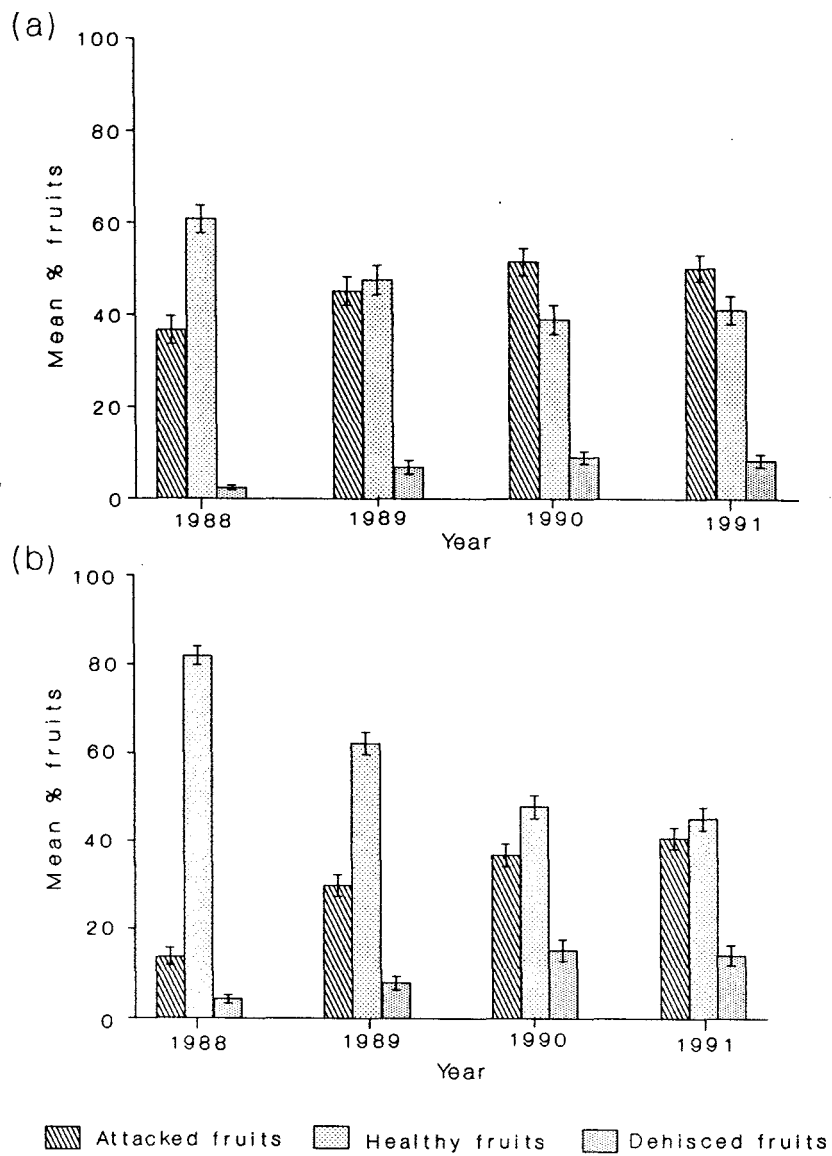


Fig. 2. The annual increase in the mean percentage of *H. sericea* fruits attacked by *C. autologa*, and the mean percentage of fruits damaged by *C. gloeosporioides*, from 1988 to 1991 at Paradyskloof and Knorhoek. Vertical bars represent standard error.

1991 level of infestation showed an increase in the mean number of fruits attacked at both sites, but no increase in the percentage of fruits attacked at Paradyskloof as the mean number of healthy fruits increased markedly at this site (Fig. 2). Possible explanations are that *H. sericea* set more fruit in 1991, or that *E. consputa*, which attacks the immature fruits, was less effective.

Total seed destruction

Based on the fruits returned to the laboratory in September 1990 4.0% of the fruits showing no emergence holes had one seed consumed and 8.5% had both seeds consumed at

Table 4. The mean percentage (\pm SE) of fruits with emergence holes, with one or both seeds consumed by *C. autologa* but without emergence holes, healthy fruits and fruits dehiscid due to *C. gloeosporioides* damage from Paradyskloof and Knorhoek in 1990.

Fate of fruits/seeds	Paradyskloof (n=3070 fruits)	Knorhoek (n=1907 fruits)
Emergence holes	51.7 (\pm 3.00)	36.8 (\pm 2.56)
One seed consumed	4.0 (\pm 1.29)	5.4 (\pm 0.85)
Both seeds consumed	8.5 (\pm 1.78)	8.4 (\pm 1.16)
Healthy fruits	26.7 (\pm 2.98)	34.0 (\pm 2.70)
Dehiscid fruits	9.2 (\pm 1.38)	15.3 (\pm 2.40)

Paradyskloof (Table 4). At Knorhoek the mean number of fruits without emergence holes but with one or both seeds consumed was 5.4% and 8.4%, respectively.

Although this larval mortality appears to be high, this is cumulative and not annual mortality. Unfortunately the cause of the mortality is obscured by the age of the fruits and the time which elapsed since entry took place. If the mean number of destroyed fruits showing no emergence holes is added to the mean number of fruits with emergence holes then the total mean seed destruction achieved by *C. autologa* at the end of 1990 at Paradyskloof and Knorhoek was 64.2% (± 3.00) and 50.6% (± 2.97), respectively.

Table 5. The effect of the fungus *C. gloeosporioides* on *H. sericea* fruits and trees at Paradyskloof and Knorhoek from 1988-1990.

Site	Year	Total fruits examined	Mean % fruits diseased (SE)	% trees diseased (SE)	% trees dead (SE)
P'kloof (n=91 trees)	1988	2583	2.5 (± 0.51)	0	0
	1989	2583	7.0 (± 1.50)	30.8 (± 4.84)	2.2 (± 1.54)
	1990	3070	9.2 (± 1.38)	24.2 (± 4.49)	14.3 (± 3.67)
Knorhoek (n=100 trees)	1988	1772	4.3 (± 0.96)	0	0
	1989	1772	7.9 (± 1.48)	32.0 (± 4.66)	1.0 (± 0.99)
	1990	1907	15.3 (± 2.40)	33.0 (± 4.70)	8.0 (± 2.71)

At the start of the study trees free from fungus were selected, but after three years 14% and 8% of the sample trees had died at Paradyskloof and Knorhoek, respectively, and some of the fruits on the remaining trees had dehisced as a result of *C. gloeosporioides* attacks (Table 5). The seeds from dehisced fruits do not necessarily contribute to the *H. sericea* population as the seed is short-lived, and high seed loss occurs if conditions are not favourable for germination. A significant proportion of seed is also consumed by granivores (Richardson & Manders, 1985). Unfortunately, the chances of larvae in fruits that dehisce moving to new fruits is remote and the larvae therefore die.

The mean loss of fruit due to the fungus increased during the present study from 2.5% and 4.3% to 9.2% and 15.3% at Paradyskloof and Knorhoek, respectively (Table 5). Dennill *et al.*, 1987 in their study, found that after two years 78.0% of the trees had died as a result of fungal damage. This mortality of trees contributed to the low *C. autologa* population levels found at Paradyskloof in 1984 and led to the suspension of the *C. autologa* programme.

In 1990 the effect of the fungus on both *C. autologa* and *H. sericea* populations was not as devastating (see Chapter 4), total mean seed destruction achieved by *C. autologa* and *C. gloeosporioides* being 73.3% (± 2.98) and 66.0% (± 2.70) for Paradyskloof and Knorhoek, respectively.

Dispersal

From the diagrammatic representation (Fig. 3) of the study sites at Paradyskloof and Knorhoek, it is clear that the

Table 6. *Carposina autologa* effect on *Hakea sericea* at 5 sites near release sites.

Site (Date)	No. of fruits	Mean % fruits with emergence holes (\pm SE)	Distance and direction from nearest release site
Franschhoek (1990)	703	10.64 (\pm 2.52)	8km South
" (1992) (33°56'S 19°09'E)	4008	34.53 (\pm 2.03)	" "
Paarl (1991) (33°50'S 19°01'E)	5171	0.00	13km West
Knorhoek dam (1991) 34°06'S 18°57'E)	2170	6.53 (\pm 1.79)	2km North
Sir Lowry's Pass (1991) (34°08'S 18°57'E)	1587	0.00	2km South-west
Jonkershoek (1990) (34°58'S 18°54'E)	28028	0.01 (\pm 0.03)	4km North-east

moth has spread throughout the 2ha sites and the distribution of emergence holes has remained consistent for both sites.

The ability of the moth to disperse over longer distances was most surprising. At Franschhoek, 10.6% of the mean accumulated fruits were found to be attacked in 1990 (Table 6). When this site was sampled again in 1992 34.5% of the mean accumulated fruits had emergence holes. This colony originated from the Wemmershoek site 8km away over the Wemmershoek mountains. The Wemmershoek site was one of the first *C. autologa* release sites in the south-western Cape (Table 1), but was felled in 1983 when *C. autologa*

population levels were still very low. The infestation levels at the other sites were disappointingly low, and it is thought that dispersal is probably wind-related. The prevailing winds are north-west when adults are present. The ability of the moth to disperse and establish successfully when population levels are low is an important factor for a biological control agent to be effective.

CONCLUSIONS

C. autologa was introduced to reduce the large quantities of canopy-stored seeds of *H. sericea*. At the end of 1990, *C. autologa* reduced the mean accumulated seeds at Paradyskloof and Knorhoek by 64.2% and 50.6%, respectively, and these figures are expected to increase even further. Despite the fact that fruits are retained in the canopy and new fruits are being added annually, the annual increase in the rate of seed destruction by *C. autologa* was found to be greater than the rate of production of new fruits by the weed, except at Paradyskloof in 1991.

Whether this level of seed predation significantly reduces the recruitment of seedlings is not known. However, the seed reduction caused by *C. autologa* will limit the quantity of seed available for regeneration or recruitment after fires, and in that sense *C. autologa* has achieved the aims for which it was introduced. Predispersal seed predation is only relevant if it reduces the seed density below levels at which the plant population will be reduced by density-dependent processes (Harper, 1977) and density-independent post-dispersal predation.

It is difficult to predict the level of predation needed to reduce the seed bank below the threshold level required to result in a decrease in the density of the plants. In the case of *Carduus nutans* it was predicted that 99.9% of the seed would have to be destroyed by *Rhinocyllus conicus* Froelich to achieve control (Sagar, 1972), although a sustained reduction of the seed around 50% was enough to achieve control (Harris, 1986).

Predation of seeds is important in the dynamics of plant populations (Janzen, 1971; Harper, 1977). Seed loss reduces the distance at which a given density of seeds occurs from the seed source, i.e. the rate of dispersal. A reduction in the seed crop of 50% will halve the number of seeds reaching any point in the dispersal range, and will alter the distance from the seed crop at which any particular density of seed will land (Harper, 1977). A reduction in the number of seeds being dispersed will result in the formation of fewer nascent foci. Satellite foci can become the paramount problem for eventual weed control, even when the main infestation is allowed to grow unimpeded (Moody & Mack, 1988).

Richardson *et al.* (1987) suggest that the success of *H. sericea*, relative to other alien *Hakea* species, arises largely from the production of relatively large numbers of viable seeds. Because seed production is the only method of reproduction, control measures aimed at reducing the seed bank, should provide the most effective means of combating *H. sericea*.

The slow establishment of *C. autologa* at Paradyskloof was attributed to a number of possible factors (Dennill *et al.*, 1987). In the following chapter, aspects of the biology

and phenology of *C. autologa* will be examined to determine what factors might have contributed to the slow establishment of *C. autologa* in South Africa.

CHAPTER 3

Factors contributing to the slow colonization of *Carposina autologa* in South Africa

INTRODUCTION

Carposina autologa was first released at Paradyskloof in 1977 and numerous releases were made up to and including 1981 (Table 1). However, when the impact of *C. autologa* on *H. sericea* was evaluated between 1982 and 1984 infestation levels were low and population levels decreased over the sampling period (Dennill *et al.*, 1987). Various factors could have contributed to the slow establishment such as biotic factors (predators, parasites, pathogens, competitors, etc.), unfavourable climatic conditions or population numbers that were below a critical level necessary for colonization.

The biology of *C. autologa* was studied in detail by Naser (1968) in Australia who found that pre-penetration mortality of young larvae was high, with only 13% successfully entering the fruits. It was considered important to investigate whether this mortality is as high in South Africa because, (a) the high pre-penetration mortality might have contributed to the slow establishment of *C. autologa* in South Africa, and (b) the redistribution of eggs, rather than the inserting of larvae directly into fruits, was considered as an alternative method of releasing *C. autologa* (Chapter 6). High pre-penetration mortality would make the method of redistributing eggs ineffective.

The main aim of the various studies reported in this chapter were (a) to study aspects of the phenology of *C. autologa* that might explain its slow colonization in South Africa, and (b) to investigate whether the pre-penetration mortality is as high in South Africa as that observed by Nesar in Australia (1968).

METHODS

Seasonal oviposition pattern, oviposition site preference and larval mortality

To determine egg and larval mortality and the seasonal egg-laying pattern, five hundred fruits were selected and tagged on seventy five, randomly selected, *H. sericea* trees at Paradyskloof shortly before the start of the egg-laying season in March. The fruits were selected at various heights and aspects on the trees. All old *C. autologa* eggshells were removed from the tagged fruits and those fruits with emergence holes noted. The fruits were examined weekly for fresh *C. autologa* eggs using a hand-held magnifying glass. The number and position of the eggs on the fruits was recorded for each fruit. The preferred oviposition sites of *C. autologa* in South Africa were then compared to those found by Nesar (1968) in Australia.

Although attempts were made to follow the fate of the eggs, this was not always possible. The eggs are very small (approximately 0.6mm x 0.7mm) and are deposited into folds and crevices on the fruits making it extremely difficult to determine the viability of the eggs or the presence of

parasitism in the field. Therefore only the presence, and the disappearance of eggs prior to hatching, was recorded.

To determine exactly how many of the larvae successfully complete their development, the tagged fruits were left on the trees until the larvae had all emerged.

The ability of moths to distinguish between healthy and attacked fruits

A number of *C. autologa* eggs were observed on *H. sericea* fruits with emergence holes in the field, suggesting that the moths might not be able to distinguish between healthy and attacked *H. sericea* fruits. Therefore, both fruits with and without emergence holes were included in the fruits sampled in the above oviposition study. The number of eggs on these fruits was used to determine what percentage of the eggs were oviposited on previously attacked fruits.

Multiple entries

Hakea sericea fruits are stored on the tree and may be oviposited on many times during the fruit's life time. Only one larva can develop per fruit since both seeds are needed to complete larval development. Larvae that expend energy entering previously attacked fruits would have greatly diminished their chances of survival. Larvae that enter fruit already occupied by another larva bring about the death of one or both larvae as the intruding larva is immediately attacked (Neser, 1968).

To determine whether more than one larva enters a fruit, all the fruits that were returned to the laboratory at the end of the study described in Chapter 2 were examined to determine the number of fruits with more than one *C. autologa* entrance tunnel. Larvae might enter an attacked fruit through the tunnel already made by a previous larva (Neser, 1968), however, it is difficult to quantify this due to the absence of visible evidence when this occurs.

Position of entry

Carposina autologa larvae enter *H. sericea* fruits at a position along the suture of the fruit (Neser, 1968; Dennill, 1987a). The position of the entry tunnel is important, since the chances of survival would be expected to be greater for those larvae entering the fruits from a position closest to the seed cavity where less energy would be expended in tunnelling to the seed cavity. Preliminary observations had shown that numerous larvae that started tunnelling far from the seed cavity were unsuccessful. Four zones of entry on the suture (Fig. 6), similar to those of Dennill (1987a), were compared. Fruits examined consisted of instances where (a) larvae had successfully reached the seed cavity, and (b) where larvae had started the entrance tunnel but failed in their attempts to reach the seed cavity.

Mortality of larvae inside the seed cavity

A number of larvae died within fruits, after having consumed one or both seeds, but without completing their exit tunnels. At Paradyskloof, 4.0% of the fruits showing no emergence holes had one seed consumed and 8.5% had both seeds consumed. At Knorhoek, 5.4% and 8.4% of fruits without emergence holes had one or both seeds consumed, respectively (Chapter 2). It was not possible to determine the cause of this mortality due to the time elapsed since entry took place. However, the fruits from the study reported in Chapter 2 were opened and the length of the uncompleted exit tunnels measured. It was expected that the length of the uncompleted exit tunnels might give an indication of the stage at which the larvae died. The excavation of the exit tunnel only commences during the third instar (Neser, 1968).

The vertical distribution of eggs on trees

The vertical distribution of *C. autologa* eggs on *H. sericea* trees was investigated for two reasons. Firstly, to ascertain whether the eggs are distributed evenly throughout the trees or not. Secondly, the redistribution of eggs was considered as an alternative method of redistributing *C. autologa* and it would prove more profitable to harvest fruits for eggs in zones where the ratio of eggs per fruit was highest.

To determine the vertical distribution of eggs, twenty *H. sericea* trees were felled at Paradyskloof towards the end

of the egg-laying season. All the fruits in each vertical 1m zone were separately removed. The fruits from each zone were examined for eggs under a stereo dissecting microscope in the laboratory, and the number of eggs and eggs per fruit recorded.

The preference of *C. autologa* for new or old fruits

To determine whether new or old fruits are preferred by *C. autologa*, all the new and old fruits (those without emergence holes) used in the study reported in Chapter 2 were dissected and the number containing live larvae recorded. The presence or absence of eggs on new and old fruits was not used to determine this preference because of the behaviour of the larvae to move off the fruits in search of more "suitable" fruits. Statistical methods are those of Snedecor and Cochran (1980).

RESULTS AND DISCUSSION

Seasonal oviposition pattern, oviposition site preference and larval mortality

Egg-laying at Paradyskloof began in early March and lasted for three months until the middle of June when it ceased (Fig. 4). The peak oviposition period was in April when 56.8% of the eggs were laid. The maximum number of eggs per fruit was eight and the average egg density 2.07 eggs per

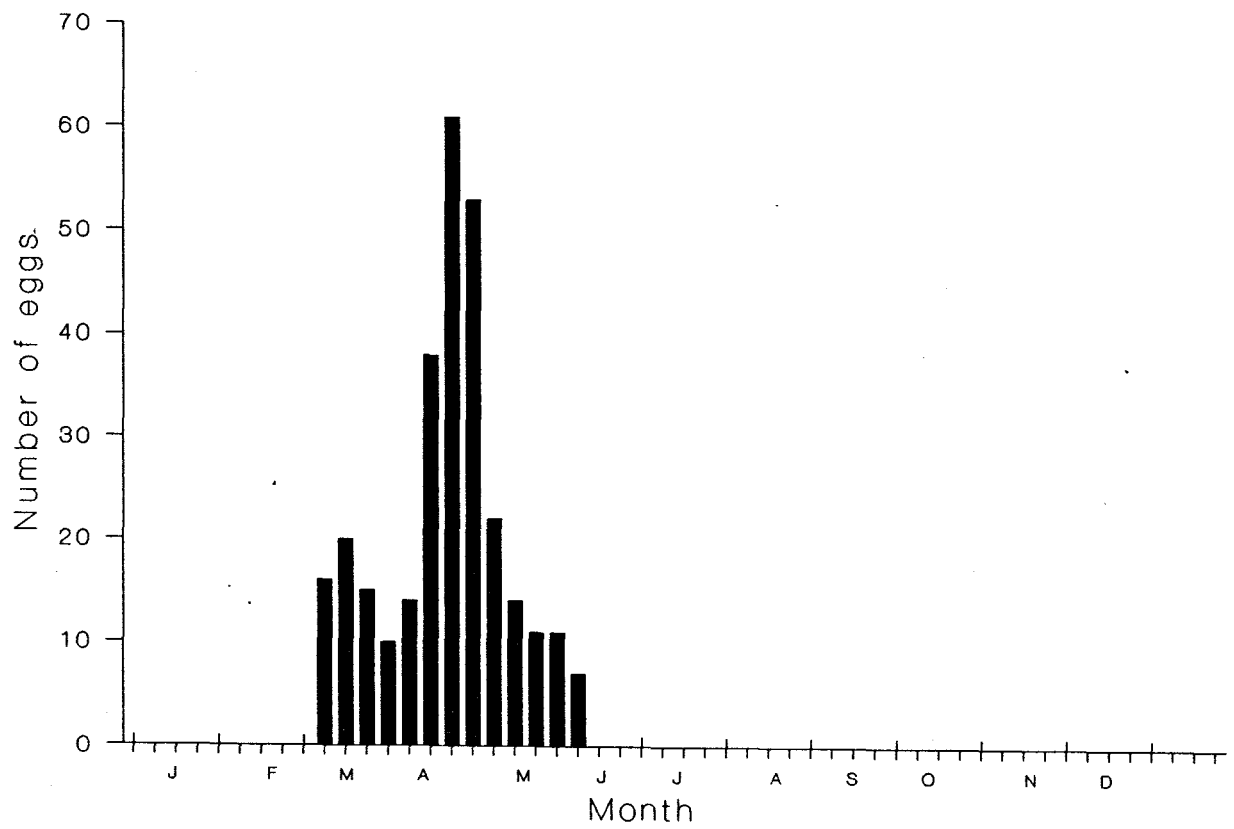


Fig. 4. The seasonal oviposition pattern of *C. autologa* at Paradyskloof during 1989.

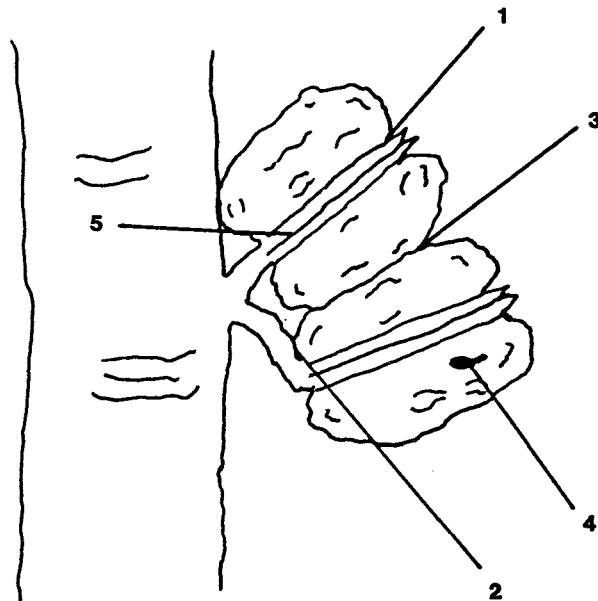


Fig. 5. A diagram of mature *H. sericea* fruits showing the preferred oviposition sites. (1) folds next to beak, (2) folds in fruit stem, (3) between touching fruit, (4) rough areas or wounds on surface of fruit, and (5) on the suture.

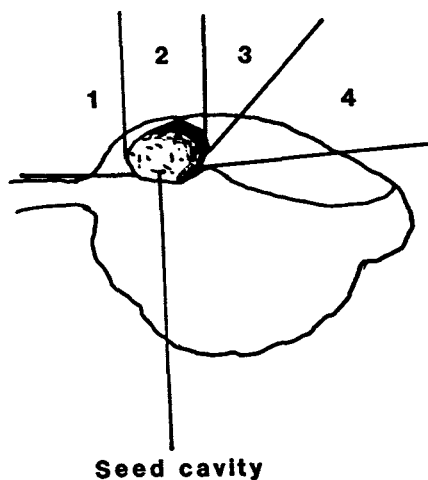


Fig. 6. A longitudinal section of a *H. sericea* fruit showing the position of the four zones on the suture where *C. autologa* enter the fruit.

Table 7. A comparison of the preferred egg-laying sites for *C. autologa* on *H. sericea* fruits at Paradyskloof and Wilson's Promontory, Victoria, Australia.

Position	Paradyskloof % eggs (n=292)	Wilson's Promontory * % eggs (n=599)
Folds next to beak	49	63
Folds in fruit stem	16	17
Between fruit and touching stem	24	9
Rough areas or wounds on surface	9	7
On suture	1	2
Adaxial groove	1	1
Egg-shells of <i>Dixoncis pictus</i>	N.a.	1

* Data from Nesar (1968)

egg-bearing fruit, fewer than the 4.97 eggs per fruit found by Nesar (1968) in Australia.

The most favoured ovipositional site on the fruits was in the folds next to the beak of the fruit, in folds in the fruit stems and between touching fruit (Table 7; Fig. 5). Eggs oviposited in folds next to the beak of the fruit or in the folds of the fruit stem are well protected. Eggs oviposited between touching fruit and stems can be damaged by abrasion when the wind blows. It is also possible to damage these eggs when harvesting fruits for eggs. These preferred oviposition sites are similar to those that Nesar (1968) found in Australia (Table 7). The moths lay their eggs in crevices and protected sites on the fruits, and not in a position closest to the seed chamber. Observations during the study confirmed that *C. autologa* prefers fruit

with crevices and protected sites for oviposition instead of smooth fruit.

During the oviposition trial 292 eggs were laid on 141 fruits by *C. autologa* (168 eggs on healthy fruits and 124 eggs on attacked fruits). Only 13.1% of the healthy fruits with eggs yielded mature larvae. Nesar (1968) found that only 13% of the estimated number of hatched larvae successfully reached the seed-cavity of *H. sericea* fruits in Australia.

Eight healthy, tagged fruits on which no eggs were oviposited also yielded mature larvae. These fruits were then removed from the trees and re-examined in the laboratory for signs of egg shells. Since no traces of egg shells were found it therefore appears as if the neonate larvae not only move off the fruits, but are able to find and successfully enter other fruits. A total of 19 or 6.5% of the eggs disappeared prior to hatching.

The ability of moths to distinguish between attacked and healthy fruit

The moths appear to be unable to distinguish between healthy and previously attacked fruits; of the 292 eggs laid, 42.5% were laid on attacked fruits. Many of these eggs will be "lost", since the neonate larvae will have to search for healthy fruit. Many of the larvae will be unsuccessful in their search and be exposed to predators and possible unfavourable weather conditions. The larvae are vulnerable to dehydration prior to entering the fruits (Nesar, 1968).

C. autologa moths also appear to prefer certain fruits for oviposition and these fruits are oviposited on regularly during the life of the fruit. As the number of attacked fruits increases so too will the number of "lost" eggs.

Multiple entries

A total of 3733 fruits were examined for more than one entry tunnel. Only 204 or 5.5% of the fruits had two entry tunnels and four or 0.1% had three tunnels. This is not considered high since these figures are not annual percentages but cumulative due to the serotinous nature of *H. sericea*. In the cases where there were multiple entry tunnels, 83.2% of the fruits had emergence holes and 2.9% contained live larvae (Table 8).

Table 8. The condition of fruits with more than one entry tunnel at Paradyskloof (n=208).

Contains emergence hole	83.2
Larva alive in fruit	2.9
Both seeds partially consumed	5.8
One seed partially consumed	5.3
Healthy fruit	1.9
Infertile seeds in fruit	1.0

Position of entry

Of the 426 fruits containing live larvae examined, 58.0% and 25.1% of the larvae entered the fruits from position 2 and 3, which are the closest routes to the seed cavity (Fig. 6; Table 9). Only 5.2% of the larvae entered the fruits from position 4, which is the longer route. Dennill (1987a), on examining fruits from Australia found that 51.7% of the larvae successfully entered the fruits from a position similar to position 2 described above and that 13.3% of the larvae entered from the longer, position 4 route.

Of the 160 fruits where the larvae were unsuccessful in their entry attempts, the trend was very similar, indicating that most of the larvae enter the fruits at a point closest to the seed cavity (Table 9).

Table 9. The percentage of *Carposina autologa* larvae successfully and unsuccessfully entering *Hakea sericea* fruits along the suture from four different zones.

Zone	1	2	3	4
% successful entry (n=426)	11.7	58.0	25.1	5.2
% unsuccessful entry (n=160)	4.4	46.9	31.2	17.5

Mortality of larvae inside the seed cavity

The length of the exit tunnel was used to obtain an indication of larval age at death. It was found that 16.0% of the larvae died before commencing the exit tunnel (Fig. 7). This therefore means that very little of the mortality occurred during the earlier larval instars as the larvae normally commence their exit tunnels during the third or fourth instar (Neser, 1968).

The length of successfully completed exit tunnels was also measured, and their length varied from 4-13mm. Very few larvae excavated their tunnels via the shorter route (Fig. 7).

The vertical distribution of eggs on trees

Most of the eggs and egg-bearing fruits were found in the 3 - 4m vertical zone of the tree (Fig. 8b & 8c). The distribution of eggs and egg-bearing fruits in the various zones did not differ significantly, except between the 0 - 1m zone which had the fewest eggs and egg-bearing fruits and the 3 - 4m zone which had the most eggs and egg-bearing fruits.

The zone with the highest mean percentage of egg-bearing fruits (32.4%) was the 4-5m zone, which was significantly different from the other zones (Fig. 8d). The mean percentages presented in Fig. 8d represent back-transformations from logit transformed means. The fruits

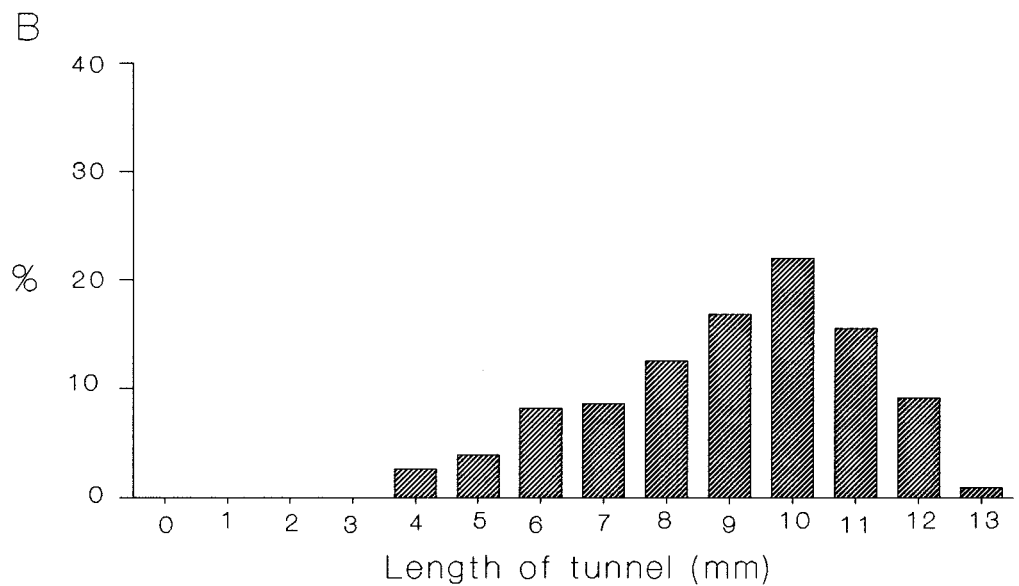
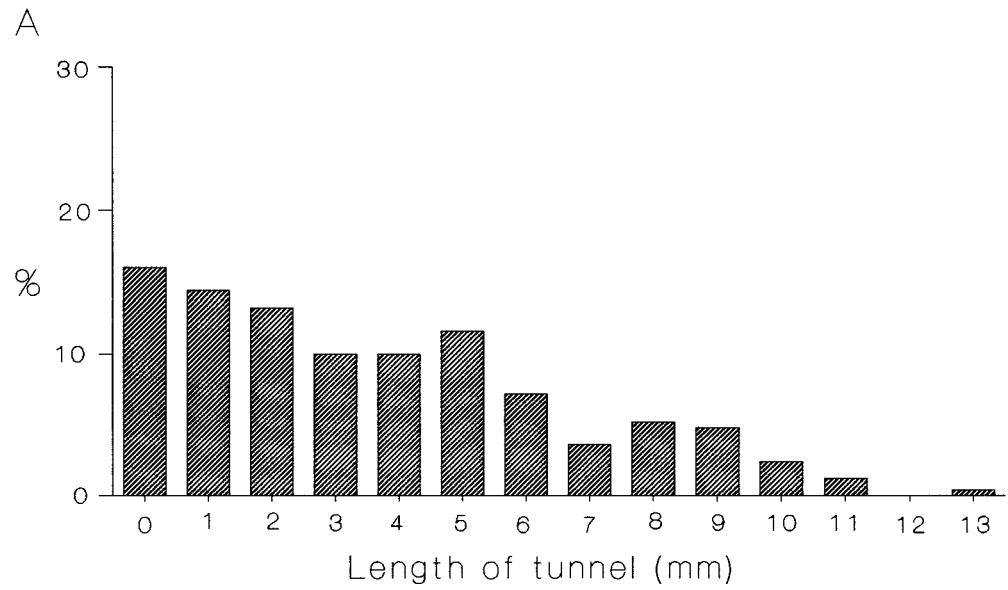


Fig. 7. The length (mm) of (A) uncompleted *C. autologa* exit tunnels when one or both seeds have wholly or partially been consumed, and (B) successfully completed *C. autologa* exit tunnels. (0 refers to the situation where the tunnel had not been started)

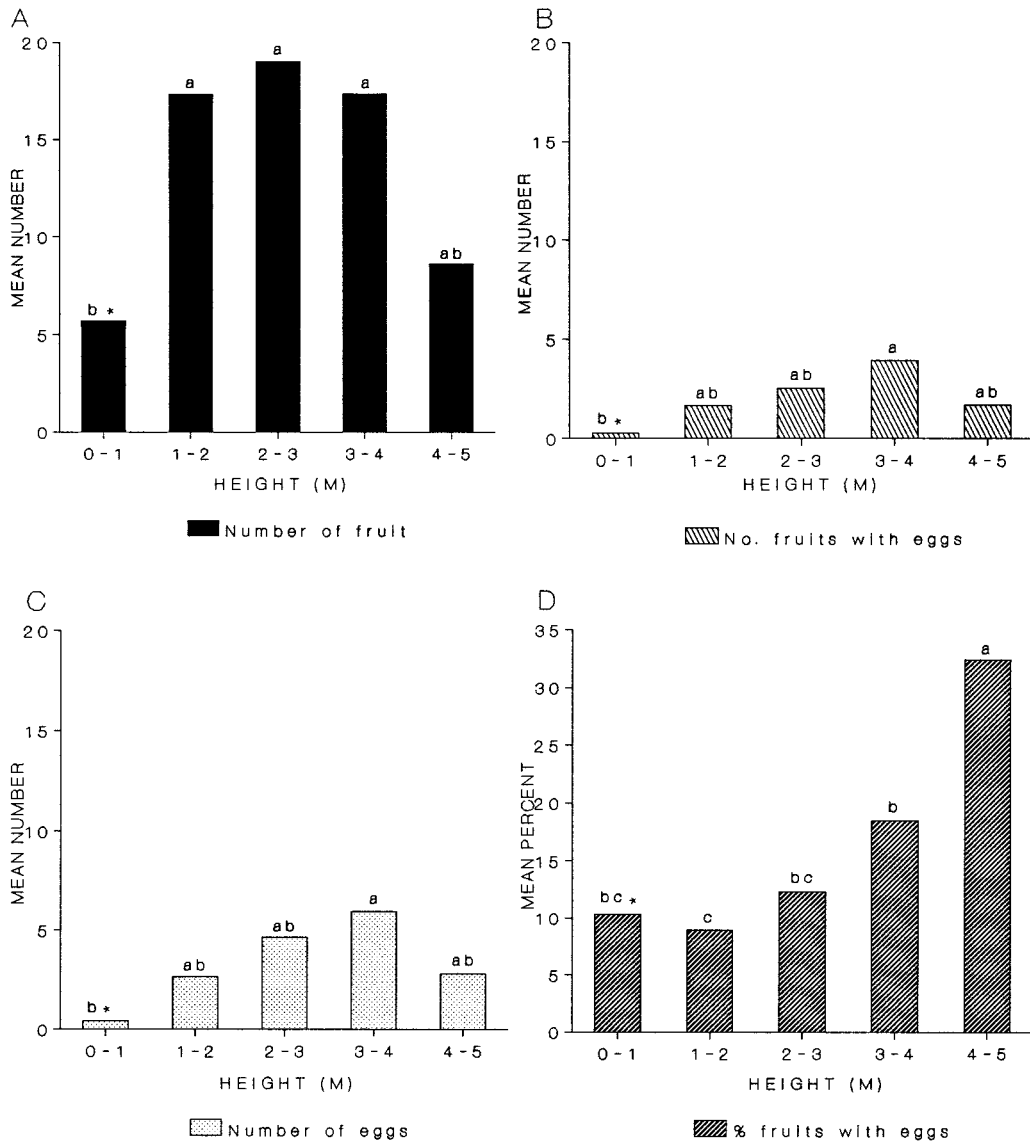


Fig. 8a. The mean number of *H. sericea* fruits per tree in each 1m vertical zone at Paradyskloof.

Fig. 8b. The mean number of egg-bearing fruits in each vertical 1m zone at Paradyskloof.

Fig. 8c. The mean number of *C. autologa* eggs in each vertical 1m zone at Paradyskloof.

Fig. 8d. The mean percentage of egg-bearing fruits in each vertical 1m zone.

* - means with the same letter are not significantly different at the 5% significance level.

situated in this zone are the newest fruits on the trees. Although this zone would yield the most eggs, it is not the most practical zone to harvest from as the fruits will be difficult to reach.

The preference of *C. autologa* for new or old fruits

At Paradyskloof, 25.4% of the new fruits and 15.9% of the older fruits yielded live larvae (Table 10). This preference for new fruits recorded at Paradyskloof was found to be highly significant ($P < 0.001$). The reverse was the case at Knorhoek as 5.2% of the new fruits and 11.7% of the older fruits yielded live larvae. This preference for older fruits at Knorhoek was also found to be significant ($P < 0.005$). This preference for older fruits at Knorhoek was most surprising as Nesor (1968) found *C. autologa* preferred new fruits in Australia.

Table 10. The number and percentage of new and old *H. sericea* fruits containing live *C. autologa* larvae from Paradyskloof (P) and Knorhoek (K).

Site	Total no. new fruits	No. (%) larvae	Total no. old fruits	No. (%) larvae	Probability of difference between proportions
P	919	233 (25.4)	1244	198 (15.9)	<0.001
K	248	13 (5.2)	1064	125 (11.7)	0.004

Although low *C. autologa* population levels at Knorhoek have resulted in more older fruits being available to the moths than at Paradyskloof, it is probably the location of the sites that have contributed most to the difference in moth behaviour. The Knorhoek site is located on an exposed north-facing slope whereas the Paradyskloof site is situated on a protected south-facing slope. During the winter months Knorhoek is exposed to strong north-westerly winds. In 1981 numerous *C. autologa* releasing trips to Knorhoek had to be aborted due to the wind blowing so strongly that larvae could not be inserted into the fruits (A.J. Gordon, unpublished results, 1981). As the new fruits are located higher up on the trees the moths will be exposed to the strong north-westerly winds at Knorhoek if they are active in the tops of the trees. The Paradyskloof site is well protected from wind and adverse weather conditions during the oviposition season and the moths do not have to seek protection lower down on the trees.

DISCUSSION

This study has highlighted a very important feature, namely the apparent inability of the moths to distinguish between healthy and previously attacked fruits. At Paradyskloof 42.5% of the eggs were oviposited on attacked fruits. There is no doubt that this will negatively affect the moth's potential as a biological control agent, as the moths will continue to oviposit on the same fruits year after year. Many of these eggs will be "lost", since the chances of all the larvae moving to, and successfully entering, new fruits is slim. In areas where *E. consputa* is effective, there will be fewer fruits available on the trees. With the

fruit being situated further apart, the chances of the larvae locating the fruits will be greatly reduced.

The aspects of the phenology of *C. autologa* reported on above, are similar to those found by Nesar (1968). The cause of the high pre-penetration mortality found in the present study, and reported on by Nesar (1968), is difficult to establish. However, it is suspected that the behaviour of the neonate larvae to move off both attacked and healthy fruits, contributes largely to this mortality. If the larvae move off the fruits in search of new fruits because the adults cannot distinguish between healthy and attacked fruits then this behaviour would serve some function. Even when eggs were released on healthy fruits, hundreds of kilometers away from existing release sites, the larvae were still found to move to new fruits (Chapter 6). The larvae are extremely delicate, and during their search for suitable fruits, are exposed to both the elements and predators.

Larval mortality also occurs, to a lesser degree, when larvae enter fruits already occupied by another larva or enter previously attacked fruits. Surprisingly few larvae were found to enter fruits already attacked despite the fact that more than one egg is laid on a fruit, and some fruits are oviposited on more than once during their lifetime. This might lead one to suspect that the larvae move off the fruits if more than one egg is oviposited per fruit. This however is not the case. Even when single eggs were attached to healthy fruits in the field the larvae still persisted in moving off the fruits (Chapter 6).

Despite the above mentioned failings, *C. autologa* has shown a remarkable ability to disperse and establish new colonies

(Chapter 2). Although these factors probably contributed to the slow establishment of *C. autologa* in South Africa, they were certainly not the only factors. In the next chapter (Chapter 4) the effect of the fungus, *C. gloeosporioides* on both *C. autologa* and *H. sericea* populations will be discussed.

CHAPTER 4

The effect of the fungus, *Colletotrichum gloeosporioides*, on the weed, *Hakea sericea* and the biological control agent, *Carposina autologa*

INTRODUCTION

Predators, parasites and pathogens have adversely influenced the outcome of many biological control programmes (Goeden & Louda, 1976). In some cases the agent has not established and in others it has not contributed to the control of the weed. Assessing the relative importance of biotic factors (predators, parasites, pathogens, competitors, etc.) is problematic (Goeden & Louda, 1976) and there is very little quantitative evidence in the literature of biotic factors influencing biocontrol projects.

The effectiveness of the biocontrol agent *Carposina autologa* is being hindered, in South Africa, by the death and die-back of its host *Hakea sericea*. The causal organism is the indigenous fungus, *Colletotrichum gloeosporioides* (Penz.) Sacc. (Morris, 1982a).

C. gloeosporioides was first noted in the south-western Cape in 1964 (Taylor, 1969). Typical symptoms of the disease are stem and branch lesions exuding quantities of colourless gum which later become reddish brown in colour (Morris, 1982b). When these lesions girdle the stem or branches, it effectively ring barks the plant causing die-back. When girdling takes place lower down the main stem or at ground

level the host plant invariably dies. The growth tips of young seedlings are also attacked, with necrosis extending down the stems killing the seedlings (Morris, 1982a).

Large numbers of plants have died, and dense stands of *H. sericea* destroyed, by the fungus (Morris, 1982b). *H. sericea* trees and branches that die as a result of fungus cause the accumulated fruits on the affected trees or branches to dehisce, and the seeds to fall to the ground. This seed loss occurs at a crucial stage during *C. autologa* larval development. Most of the infected plants die and release their seeds between October and January (Richardson & Manders, 1985). Larval development at this stage is well advanced. If the fruits dehisce when *C. autologa* larvae are almost mature, then the mature larvae might still be able to complete their development. If the larvae are immature then they will die as the chances of their finding and entering new fruits is remote.

The fungus is presently being utilized for the biological control of *H. sericea*. Various methods of culturing and inoculating plants have been successfully developed. These include wound inoculations and knapsack and aerial applications of spore suspension of the fungus (Morris, 1983). A more recent development is the application of a dried preparation of fungal-colonized wheat bran onto young seedlings (Morris, 1989).

Richardson and Manders (1985) constructed a transition matrix model to predict the progression of the fungus. They predicted that the fungus would destroy 82% of the *H. sericea* population at their study site at Vergelegen (34°02'S 18°56'E) near Somerset West after ten years. Unfortunately this model was based on research undertaken at

one site only and might not be applicable to all stands of *H. sericea*.

During an earlier study to evaluate the impact of *C. autologa* on *H. sericea* at Paradyskloof and Stellenbosch Mountain, many of the sample trees died due to fungal attack (Dennill *et al.*, 1987). This contributed to the suspension of further evaluative work and the *C. autologa* project.

The effect of the fungus on *H. sericea* at *C. autologa* release sites might have been largely responsible for the slow establishment of *C. autologa* in the south-western Cape. It is planned to redistribute *C. autologa* throughout the range of the weed. If the fungus proves to be as devastating as predicted by Richardson and Manders (1985) and as virulent in all regions within South Africa, then further releases of *C. autologa* will prove to be a futile exercise. It is therefore essential to investigate what impact the fungus will have on *H. sericea* and *C. autologa* populations.

The aims of the studies reported on in this chapter were (a) to determine the degree of infection and progression of the fungus at *C. autologa* releases sites at Paradyskloof and Knorhoek and (b) to determine the effect the fungus has on *C. autologa* populations.

METHODS

The degree of infection and progression of the fungus

To obtain an estimate of the percentage of trees infected with fungus, ten transects, 100m long and 20m apart, were laid out across dense stands of *H. sericea* at Paradyskloof and Knorhoek. Points were located at 10m intervals along each transect. The area around each point was divided into four 90 degree quarters of the compass. The nearest living *H. sericea* tree in each quarter was selected and tagged. The presence or absence of fungus on each tree was recorded. In this way 359 and 400 trees were sampled at Paradyskloof and Knorhoek, respectively. The plants were inspected annually for signs of fungal infection and any mortality of trees recorded.

For more detailed study of the effect of the fungus on individual trees, the nearest fungus-infected tree to each located point of the four was selected and permanently tagged. In this way 84 and 95 trees were selected at Paradyskloof and Knorhoek, respectively. The height and position of any lesions on the main stem or side branches were recorded. These trees were inspected annually from 1988 to 1991. During each observation the previous seasons lesions were inspected to see if they were still active, and the presence of any new lesions recorded. For easier representation of the results the above data was transformed into classes similar to those used by Richardson and Manders (1985) as follows: 1 = tree healthy; 2 = cankers on branches but not on the main stem; 3 = cankers on the upper half of the main stem; 4 = cankers on the lower half of the

main stem; 5 = plant dead. These classes differ to those of Richardson and Manders (1985) in that a class for healthy trees has been included and a distinction made between fungus occurring in the lower and upper half of the main stem. The reason being that fungus in the lower half of the main stem appears to have a more devastating effect on the tree than when the fungus occurs on the upper half of the tree. The presence of dead leaf tips was excluded since the effect of dead leaf tips on mature plants was found to be negligible.

The effect of fungus on the canopy-stored seeds

The number of fruits that dehisce as a result of fungus will have a detrimental effect on any *C. autologa* larvae occurring in those fruits. To obtain an indication of the percentage of fruits that dehisce annually, the number of healthy and dehisced fruits on the sample trees were recorded annually.

RESULTS AND DISCUSSION

The degree of infection and progression of the fungus

The fungus was found to be present at both Paradyskloof and Knorhoek, with only 42.1% and 33.0% of the trees being healthy, respectively, in 1988 (Fig. 9). Although more trees were infected with the fungus at Knorhoek, only 16,3%

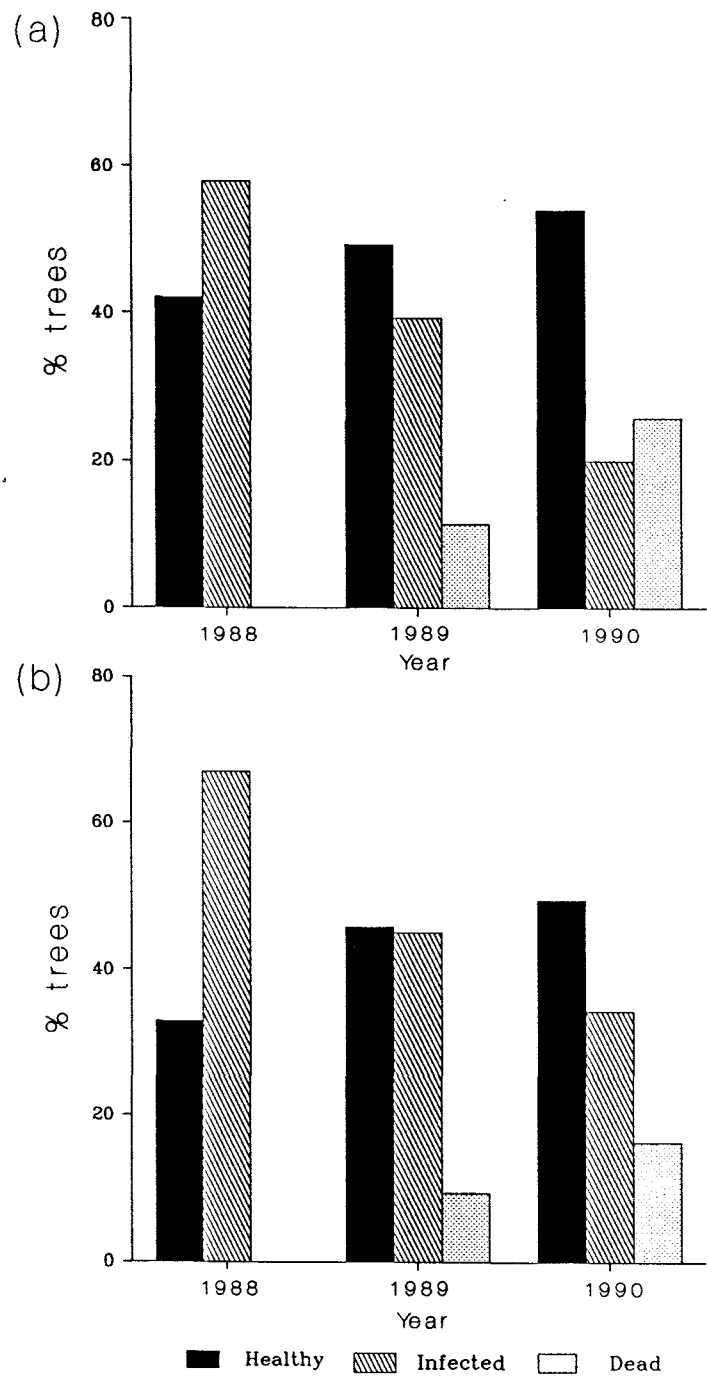


Fig. 9. The percentage healthy, fungus-infected and dead *H. sericea* trees at Paradyskloof (a) and Knorhoek (b) from 1988 to 1990.

had died after two years compared to the 25.9% at Paradyskloof (Fig. 9).

The detailed study of fungus-infected trees showed that 64.3% of the sample trees at Paradyskloof fell into infection state 4 *i.e.* fungus on the bottom half of the main stem, in 1988 (Fig. 10 & 11). The following year, 38.1% of the trees recovered with no visible signs of infection and 15.5% of the trees died. By 1991 48.8% of the trees had died, with 33.3% of trees remaining fungus free. At Knorhoek, only 40% of the trees fell into infection state 4. The following year, 36.8% of the fungus infected trees recovered and 8.4% of the trees died. By the end of the study only 15.8% of the trees died with 50.5% having recovered.

The differences in the degree of infection and mortality of trees between the sites can largely be attributed to the locations of the sites. Paradyskloof is situated on a cooler south-facing slope, and Knorhoek on a drier north-facing slope. Development of the fungus is enhanced by cooler moist conditions (Morris, 1982b).

According to the model of Richardson & Manders (1985) the predicted mortality of plants after 3 years would be in the vicinity of 38%. This prediction was exceeded at Paradyskloof as 48.8% of the trees had died whereas only 15.5% of the plants had died at Knorhoek. In the study by Richardson & Manders (1985), all of the trees were infected at the start of the study and none of the sampled trees regressed an infection state. In the present study many of the trees recovered, even those in infection state 4.

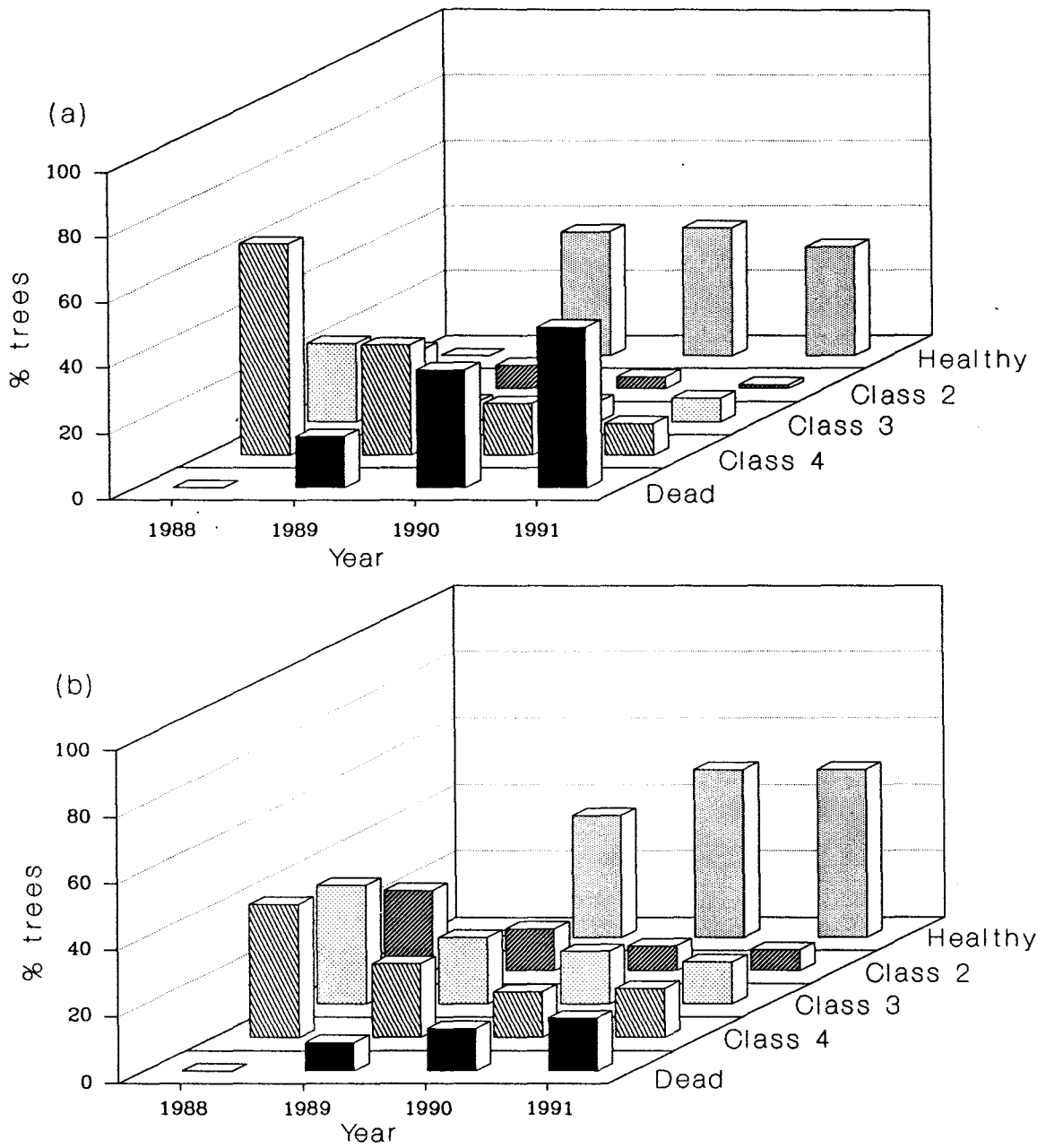


Fig. 10. The percentage of *H. sericea* trees in each infection state at Paradyskloof and Knorhoek.

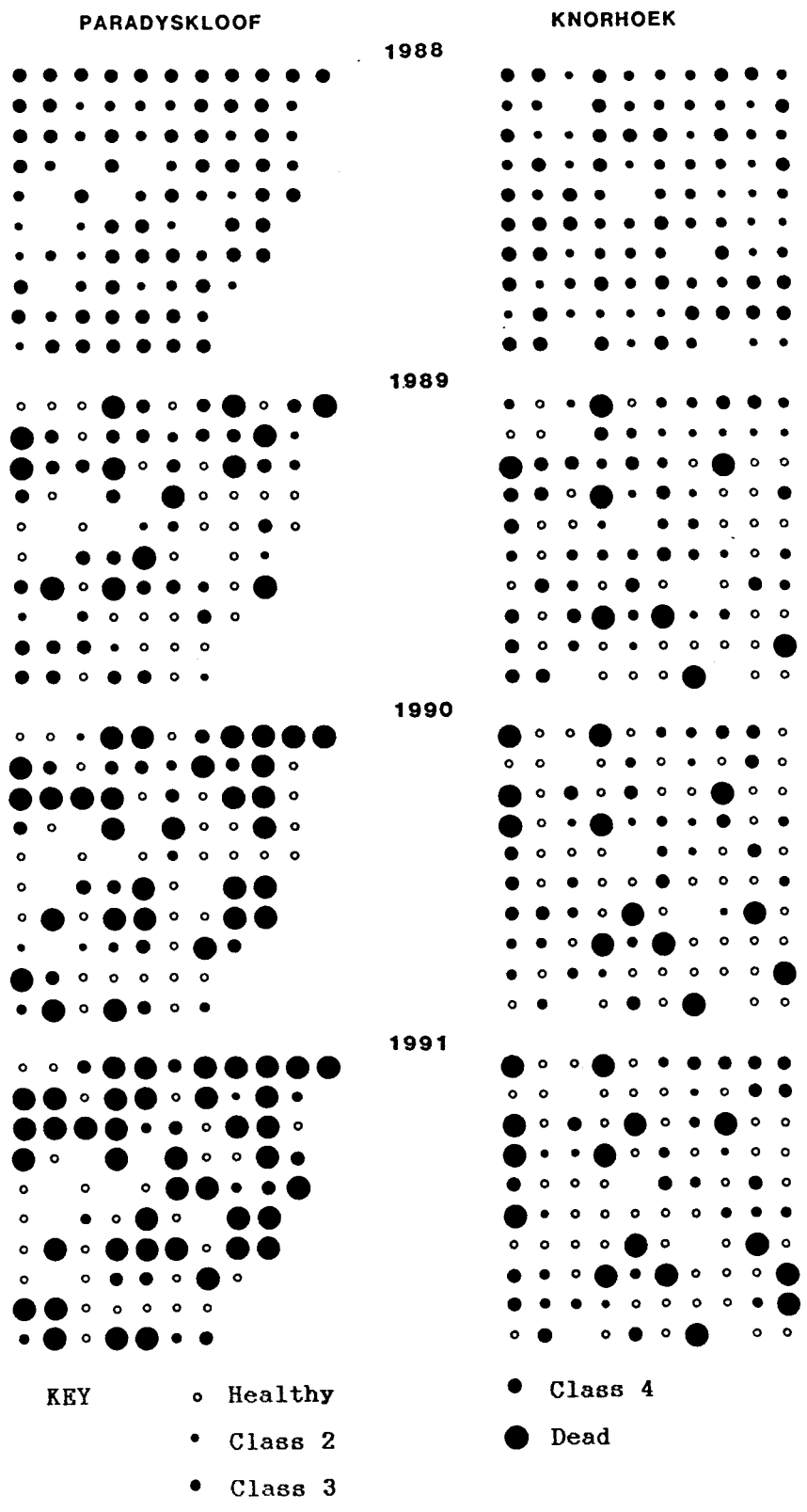


Fig. 11. A comparison of the changes in the infection states on marked *H. sericea* trees at Paradyskloof and Knorhoek from 1988 to 1991.

The timing of infection is important, since if it occurs late in the season the chances of the trees recovering is far greater (M.J. Morris, personal communication, 1992).

The effect of fungus on the canopy-stored seeds

In 1988, 16.4% and 11.5% of the fruits on sampled trees had dehisced at Paradyskloof and Knorhoek, respectively. The following year this increased to 31.3% and 20.6% for the two sites, respectively. The following year 49.7% of the seeds had dehisced at Paradyskloof and 29.4% at Knorhoek (Fig. 12). Since fruits are being lost annually on fungus infected trees, an equivalent proportion of the *C. autologa* population is also being lost.

DISCUSSION

The fungus has probably contributed to the slow establishment of *C. autologa* at Paradyskloof and to a lesser degree at Knorhoek. At low *C. autologa* population levels a high incidence of fungus can have a devastating effect on the establishment of the agent. Death of plants as a direct result of fungus and the subsequent release of seeds is largely confined to the period October to January (Richardson & Manders, 1985). However, peak emergence of larvae occurs in February and March, and therefore larval development might not be advanced enough for the larvae to pupate. The selection of release sites will therefore be crucial when releasing *C. autologa* and releases should

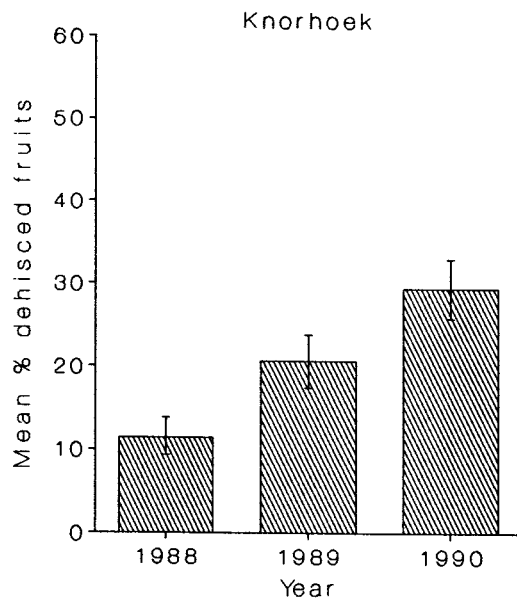
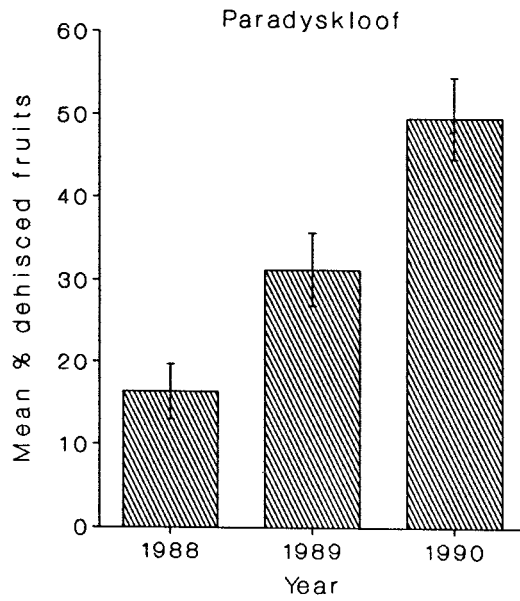


Fig. 12. The mean percentage dehisced fruits on fungus-infected *H. sericea* trees at Paradyskloof and Knorhoek from 1988 to 1990. Vertical bars represent standard error.

be made in areas where the incidence of fungus is low or absent.

The transition probability matrix derived by Richardson & Manders (1985) was only undertaken at one site. This site was fairly unique in that all the trees were infected and the fungus always progressed from one state to the next. Many of the sampled trees in the present study regressed from one state to another at both Paradyskloof and Knorhoek.

The combined effect of *C. autologa* and *C. gloeosporioides* will contribute to the control of *H. sericea* so long as the fungus does not reach epidemic proportions. The combined effect of *C. autologa* and *C. gloeosporioides* resulted in only 26.7% and 34.0% of the accumulated seeds remaining healthy at Paradyskloof and Knorhoek, respectively (Chapter 2). The seeds released as a result of the fungus will only germinate in mid-winter in the south-western Cape. As the seeds are released between October and January many of them are likely to be consumed by granivores prior to germination.

The development of *C. gloeosporioides* as a mycoherbicide will definitely have an adverse affect on *C. autologa* populations. However, the effectiveness of the mycoherbicide still has to be evaluated throughout the range of *H. sericea*. Initial studies have shown that the best results are obtained when used against seedlings, with the timing of application all important (Morris, 1989). In an integrated control program the possibility of *H. sericea* reserves, similar to those used for *E. consputa*, should be considered. However, despite the detrimental effects of *C. gloeosporioides* and those aspects of its own phenology that limit its effectiveness (Chapter 3), *C. autologa* has

still managed to contribute to a reduction in the accumulated seed-store of *H. sericea*.

CHAPTER 5

Have insect-host plant relationships influenced estimation of the efficacy of the biological control agent *Carposina autologa*?

INTRODUCTION

The impact of the biocontrol agent *Carposina autologa* on *Hakea sericea* was first evaluated in 1982 (Dennill *et al.*, 1987). This study was undertaken at two sites in the southwestern Cape (Paradyskloof and Stellenbosch Mountain). Due to the abundance of fruits on the trees at these sites, it was deemed necessary to design a sampling technique for the taking of representative fruit samples. Six trees were felled and the number of fruit in each vertical 1m zone recorded, noting the number with *C. autologa* emergence holes. The results showed that although only 7,3% of the fruits sampled were located in the bottom metre, 38,2% of the attacked fruits occurred in this zone. On the basis of these results only the bottom metre and the bottom one-and-a-half metres of the trees were sampled at Paradyskloof and Stellenbosch Mountain, respectively. The results from these studies showed that *C. autologa* infestation levels were low, and in fact decreased during the sampling period. It has, however, subsequently been shown that *C. autologa* infestation levels have increased at Paradyskloof (Chapter 2). This raises the question "Did sub-sampling not result in an underestimation of the efficacy of *C. autologa* in the study reported by Dennill *et al.* (1987)?"

The second part of this chapter is allocated to the determination of the "ecological" success of *C. autologa*. The data presented in Chapter 2 has shown that *C. autologa* reduced the mean percentage accumulated fruits by 50.4% and 40.7% at Paradyskloof and Knorhoek, respectively. However, ecological information resulting from the relative timing of fires and fruit set was not taken into account when accessing the success of *C. autologa*.

The aim of the studies reported in this Chapter were (a) to investigate the effect sub-sampling has on the interpretation of the results of the efficacy of *C. autologa* and (b) to determine the "ecological" success of *C. autologa*.

THE EFFECT OF SUB-SAMPLING IN THE DETERMINATION OF THE EFFICACY OF *C. AUTOLOGA* AS A BIOCONTROL AGENT

METHODS

To demonstrate that infestation levels had increased at Paradyskloof and Knorhoek (Chapter 2), the whole tree was sampled to circumvent the problems of sub-sampling. However, to test whether sub-sampling might not have influenced the results obtained by Dennill *et al.* (1987), the trees sampled in Chapter 2 were divided into vertical 1m zones. Each vertical 1m zone was permanently demarcated on the main stem with paint. All the fruits in the various zones were counted and examined for *C. autologa* emergence holes annually from 1988 to 1990 at both Paradyskloof and Knorhoek. At the end of the study, in September 1990, all

the fruits in the respective zones were removed from the trees and examined for *C. autologa* larvae. This figure was then used as an indication of the population increase for 1991.

Regressions are used to determine if there is a relationship between the percentage attacked fruits over time for different heights and for the whole tree at both Paradyskloof and Knorhoek. Statistical methods are those of Snedecor and Cochran (1980).

RESULTS

Sampling the lower metre at Paradyskloof and Knorhoek would not have adversely influence the above results. At both Paradyskloof and Knorhoek there was no significant difference ($P = 0.05$) in the slope between the percentage attacked fruits in the 0-1m zone and the percentage attacked fruits for the whole tree (Fig. 13; Table 12). The only zone that differed significantly from that of the whole tree was the 3-4m zone at Paradyskloof.

Although the intercept of the 0-1m zone at Paradyskloof was lower than that of the whole tree, this difference was not significant. At Knorhoek the intercept of the 0-1m zone was slightly higher than that of the whole tree with a very similar slope (Fig. 13).

However, a true indication of what is happening on the trees at these sites would not have been obtained if only the

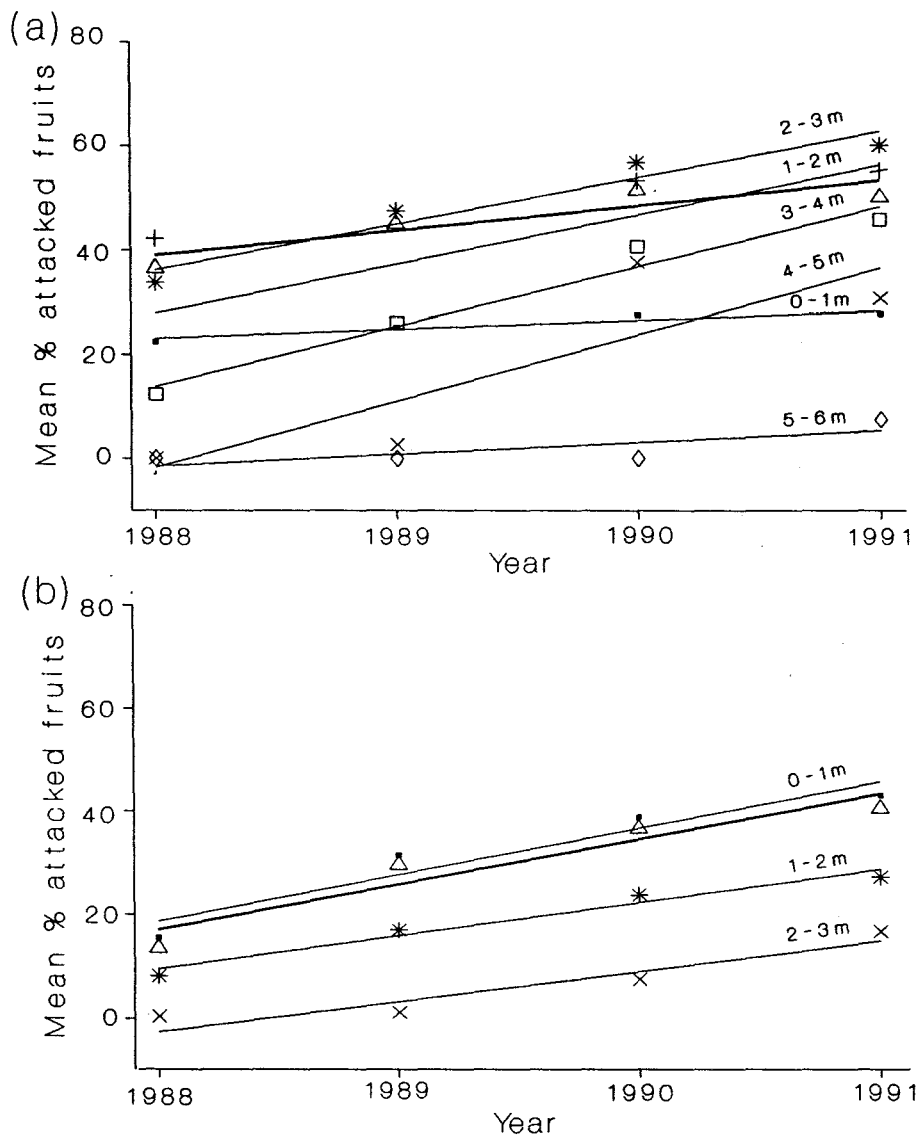


Fig. 13. Linear regressions of the annual increase in the percentage accumulated *H. sericea* fruits attacked by *C. autologa* in vertical 1m zones at Paradyskloof (a) and Knorhoek (b) from 1988 - 1991. The bold lines represent the percentage attacked fruits for the whole tree. (See Table 11 for regression equations).

Table 11. Regression equations of percentage attacked *H. sericea* fruits (Y) on year (X) for different heights and for the whole tree at Paradyskloof and Knorhoek (See Fig. 13).

Height	Regression equation	
	Paradyskloof	Knorhoek
0-1m	Y = 21.2 + 1.8X (4.24) (1.55)	Y = 9.7 + 9.0X (3.12) (1.14)
1-2m	Y = 38.4 + 4.5X (4.46) (1.63)	Y = 3.1 + 6.4X (3.48) (1.27)
2-3m	Y = 27.3 + 8.9X (4.88) (1.79)	Y = -8.4 + 5.8X (6.83) (2.38)
3-4m	Y = 2.4 + 11.5X (6.44) (2.35)	
4-5m	Y = -14.6 + 12.8X (11.92) (4.33)	
5-6m	Y = -3.8 + 2.3X (28.58) (10.44)	
Tree	Y = 34.2 + 4.8X (3.66) (1.34)	Y = 8.2 + 8.8X (2.93) (1.07)

Table 12. A comparison between regression coefficients of percentage fruits attacked by *C. autologa* on years in the various vertical 1m zones and the whole tree at both Paradyskloof and Knorhoek.

Height	Paradyskloof		Knorhoek	
	Intercept	Slope	Intercept	Slope
Tree v 0-1m	ns	ns	ns	ns
Tree v 1-2m	ns	ns	ns	ns
Tree v 2-3m	ns	ns	*	ns
Tree v 3-4m	*	*		
Tree v 4-5m	*	ns		
Tree v 5-6m	ns	ns		

* = a significant difference at the 5% level
 ns = no significant difference at the 5% level

bottom metre was sampled. For example (Fig. 14), although half the available fruits at Knorhoek would be sampled with the lower metre and thus trends effectively detected, at Paradyskloof less than 10% would be sampled and thus any trends difficult to detect. Furthermore, most of the new fruits are being added to the upper half of the tree with very few being added in the 0-1m zone (Fig. 15). Similarly, the number of fruits being attacked annually in the 0-1m zone has decreased considerably at Paradyskloof and starting to decline at Knorhoek (Fig. 15).

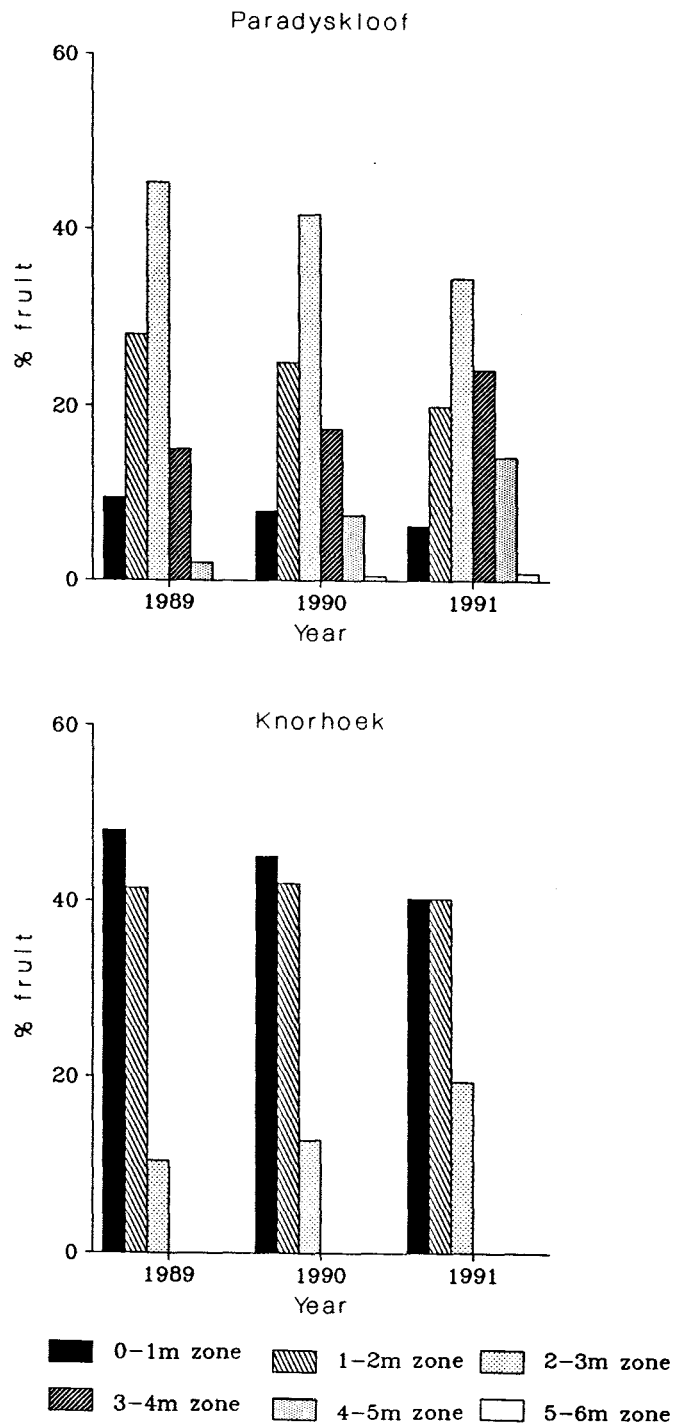


Fig. 14. The vertical distribution of fruits on *H. sericea* trees at Paradyskloof and Knorhoek from 1989 to 1991.

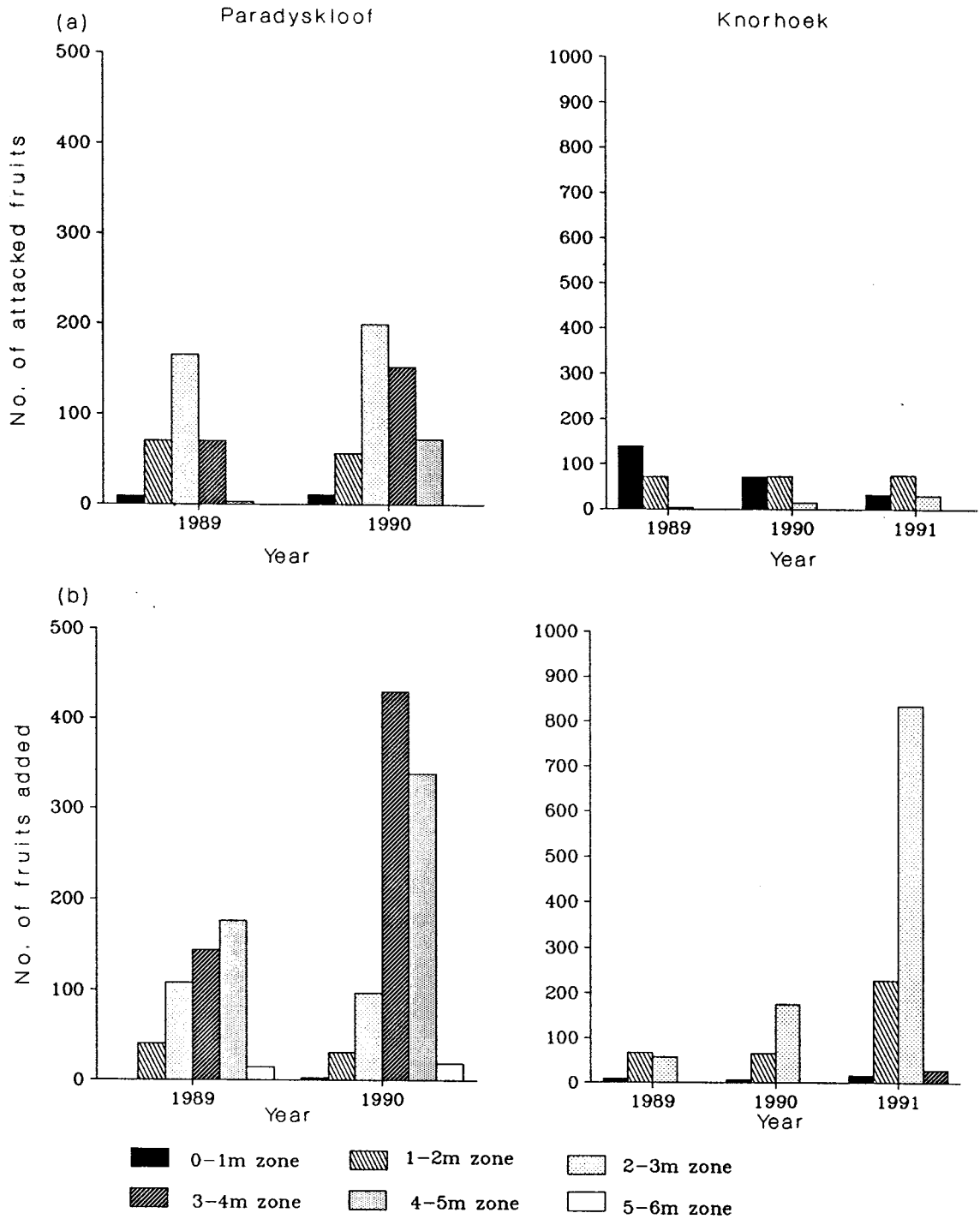


Fig. 15. The annual increase in the number of (a) *H. sericea* fruits attacked by *C. autologa* and (b) the new fruits added to the canopy in vertical 1m zones at Paradyskloof and Knorhoek.

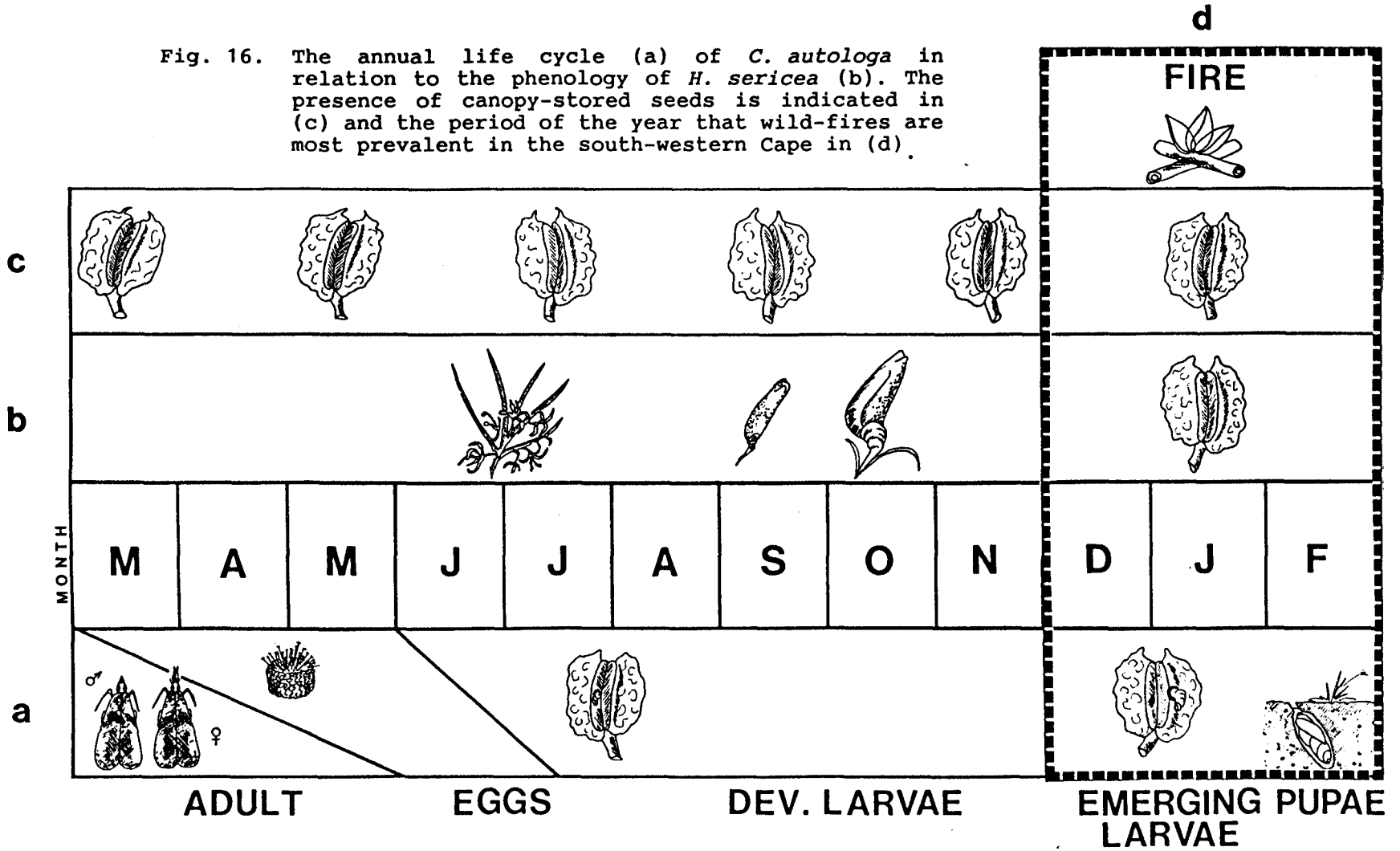
THE "ECOLOGICAL" SUCCESS OF *C. AUTOLOGA*

The impact of *C. autologa* on the canopy-stored seeds of *H. sericea*, reported in Chapter 2, was determined in March each year after the pupae had completed their development and shortly before the onset of the next fruit set. However, host-plant relationships and ecological information was not taken into account when determining the success of *C. autologa*. The annual life cycle of *C. autologa* in relation to the phenology of *H. sericea* is depicted in Fig. 16. Oviposition takes place between March and May, shortly before *H. sericea* commences flowering in July/August. Fruit development is fairly rapid with the fruits being full grown by December. At this stage the larvae are almost mature and ready to pupate in the soil.

The seeds of *H. sericea* are borne in heat-resistant follicles and are released *en masse* after fires. Periodic wild-fires are a feature of the fire-adapted, mountain fynbos vegetation (Bond, 1980) invaded by *H. sericea*. Wild-fires in the south-western Cape are generally concentrated in summer (December, January and February) (van Wilgen, 1981b). It is at this stage that the fruits of the latest seed crop mature (Fig. 16b) and these seeds are therefore available for recruitment.

H. sericea, in South Africa, relies entirely on seed for regeneration (Fugler, 1979). The timing of new fruits, moths and fire means a proportion of the fruits will never be attacked *i.e.* be available to the moths. If the latest

Fig. 16. The annual life cycle (a) of *C. autologa* in relation to the phenology of *H. sericea* (b). The presence of canopy-stored seeds is indicated in (c) and the period of the year that wild-fires are most prevalent in the south-western Cape in (d).



seed crop is taken into account when assessing the efficacy of *C. autologa*, it affects the interpretation of the success of the agent. The mean percentage damage at Paradyskloof and Knorhoek in 1990 was calculated simply on the basis of the proportion of attacked fruits.

The difference between the "theoretical" and "ecological" result is dependent on the number of fruits being added to the canopy. During the present study, *C. autologa* succeeded in destroying more fruits than the annual increment of new fruits at Paradyskloof until 1990 (Chapter 2). However, the annual increment of fruits in 1990 exceeded the number attacked the following year (Fig. 15), resulting in a decrease in the mean percentage attacked fruits for 1991. The situation at Knorhoek was similar, with the number of attacked fruits exceeding the annual increment for the duration of the study (Chapter 2). However, at the end of 1991 there was a sharp increase in the number of fruits added to the canopy at Knorhoek (Fig. 15), and a decline in the mean percentage of attacked fruits for 1992 is predicted.

DISCUSSION

The observations reported above show that the slow establishment at Paradyskloof and Stellenbosch Mountain reported by Dennill *et al.* (1987) cannot be attributed to the sampling technique used by them to evaluate the efficacy of *C. autologa*. However, although sub-sampling is not statistically incorrect, it is recommended that the whole tree be used for future evaluation studies in order to

obtain a better understanding of the behaviour of the agent and its host.

The implications of part of each seed crop escaping attack by *C. autologa* and being available for recruitment, will influence the contribution of *C. autologa* to the biological control of *H. sericea* project in the south-western Cape. Since recruitment is linked to fires, and fires occur at a stage when the latest seed crop has escaped attack by *C. autologa* means that *C. autologa* will never be able to effectively control *H. sericea*. One seed crop will always be available for regeneration. The percentage germination of first year seed is 90% (Sommerville, 1977).

The timing of fires will play a crucial role in both the reproductive success of *H. sericea* and on *C. autologa* populations. A fire in spring would result in fewer seeds being available for recruitment because (a) the fruits of the most recent seed crop would not have developed sufficiently, and the only seeds available for recruitment would be those seeds already exposed to *C. autologa* and (b) the seeds released would be exposed to predators (rodents and birds) and pathogens for an extended period in the south-western Cape as peak germination takes place in midwinter.

A spring or summer fire would have a devastating effect on *C. autologa* populations in the path of the fire. Although the larvae would be well protected within the heat-resistant fruits, the larvae would die after the fruits dehisce as they would be unable to complete their development. The only fire that *C. autologa* will have a realistic chance of surviving would be a late summer fire when moths are present.

Neser (1968) suggests that the specialized nature of *C. autologa* coupled with features of the fruits indicate a very long association with the plant, probably even from its more primitive phases. The synchronization of *C. autologa* with its host plant described above, if it also occurs in the native distribution of the species, have ensured that there is no over-exploitation of *H. sericea* by *C. autologa*. It therefore appears that *C. autologa* and *H. sericea* might have evolved a homeostasis situation in which both can co-exist without being adversely destructive to each other. This long association with *H. sericea* could hamper the degree of control that could be achieved by *C. autologa*. The selection of agents with a long association between the host and the agent have been questioned by some biocontrol practitioners (Hokkanen & Pimental, 1984; Dennill & Moran, 1989; Dennill & Hokkanen, 1990). Dennill & Hokkanen (1990) suggest that the achievement of success in biocontrol is dependent on both the release of the agent from its natural enemies and the degree of homeostasis between the host and the agent. Fortunately, in South Africa, the effect of the latest seed crop escaping predation by *C. autologa* is partially neutralized by *E. consputa*. *E. consputa* attacks the immature fruits of *H. sericea* thereby reducing the number of seeds being added to the seed store annually. At a study site at Goudini (33°40'S 19°15'E) in the southwestern Cape, the annual fruit loss increased to 81% after the introduction of *E. consputa* (Kluge, 1983). A chemical exclusion study carried out at the same site confirmed that *E. consputa* was responsible for up to 86% of the total fruit mortality (Neser & Kluge, 1985).

If an additional agent is required for the biological control of *H. sericea* then an agent that can further reduce

the number of fruits added to the canopy should be considered.

CHAPTER 6

The redistribution of the hakea seed-moth, *Carposina autologa*, in South Africa.

INTRODUCTION

The hakea seed-moth, *Carposina autologa*, was first introduced from Australia for the biological control of *Hakea sericea* in 1970. Between 1970 and 1979 attempts at establishing *C. autologa* consisted of releasing neonate larvae directly onto *H. sericea* fruits in the field and releasing moths into walk-in cages erected over *H. sericea* plants. Although several releases were made over this period they were small and did not yield a viable field colony.

After 1979 a new system was developed that involved inserting larvae directly into *H. sericea* fruits in the field. Although this method yielded the best results it was not without its problems (Dennill, 1987a). It was labour intensive, time consuming and not considered a practicable method of release for use in inaccessible areas. When it became apparent in 1989 that *C. autologa* was contributing to a reduction in the canopy-stored seeds of *H. sericea* (Chapter 2) it was decided to redistribute *C. autologa* throughout the South African range of the weed. A major objective was to establish *C. autologa* in the southern Cape where the worst infestations of *H. sericea* occur. This therefore necessitated a more practicable and less labour intensive method of release.

A factor contributing to the slow establishment of *C. autologa* in South Africa was the indirect effect of the fungus, *Colletotrichum gloeosporioides* (Chapter 4). To improve the chances of establishment, selected release sites would have to be relatively free of fungus.

Another factor that is becoming increasingly important is the financial implications of biocontrol. Biological control programmes in South Africa used to be wholly funded by central government, however since the inception of the Agricultural Research Council the programmes are only partially funded. The overseas exploration and specificity testing of suitable candidates for the biological control of *H. sericea* have been completed. It will, however, be necessary to recover the costs of collecting and redistributing *C. autologa*.

The aims of the study reported in this chapter were (a) to develop and evaluate an alternative method of release, (b) to earmark potential release sites and determine the incidence of fungus at each of them, (c) to release *C. autologa* throughout the South African range of the weed, (d) to evaluate the establishment of *C. autologa* at these sites and (e) make an assessment of the costs of redistributing *C. autologa*.

MATERIALS AND METHODS

Evaluation of the release method

The method developed to redistribute *C. autologa* was to attach egg-bearing follicles to healthy fruits in the field. To test this technique small releases were made at seven localities in the southern and south-western Cape.

Hakea sericea fruits were harvested at Paradyskloof during the egg-laying period in June 1990. The fruits were returned to the laboratory and inspected under an illuminating magnifier for eggs. The egg-bearing fruits were split in half along the suture of the fruit and the follicle with eggs kept. The egg-bearing follicles were then taken to the field and attached to healthy fruits. Although splitting the fruits involved additional work, follicles were used instead of whole fruits because, (a) the follicles are easier to attach than whole fruits, and (b) follicles eliminate the possibility of neonate larvae entering the attached fruit rather than the healthy fruit.

The follicles were attached to healthy fruits using "Bostik marine sealer" which is known not to be toxic to *C. autologa*. Care was taken not to attach the follicle to or near the suture of the fruit as the larva enters the fruit at a point along the suture.

One hundred follicles with one egg per follicle were attached to healthy *H. sericea* fruits at each of seven localities in the south-western and southern Cape (Fig. 17). Approximately three months later, the fruits with attached

egg-bearing follicle (the release fruits) were removed from the trees and returned to the laboratory. The fruits were opened and inspected for healthy *C. autologa* larvae or signs of attempted entry by the larvae.

The incidence of fungus at potential release sites

To improve *C. autologa* establishment, potential release sites were surveyed prior to release to determine the incidence of naturally occurring fungus. Thirteen *H. sericea* infestations were selected throughout the known range of the weed in South Africa as potential release sites (Fig. 18). For site details and map coordinates see Table 18 at the end of this Chapter.

At each of the sites a 100m transect was laid out across the infestation. At 10m intervals along the transect a random point was obtained at right angles to the transect. The nearest *H. sericea* tree in each quarter of the compass around each random point was sampled. In this way forty trees were sampled at each locality. The density of the trees at each site was calculated using the point-centered quarter method (Cottam & Curtis, 1956). The stem circumference, height and number of mature *H. sericea* fruits on each tree was also recorded. Each of the sample trees was inspected for signs of lesions and/or gum exudation and assigned a ranking as follows: 1 = plant healthy; 2 = lesions on branches but not on the main stem; 3 = lesions and/or gum exudation in the upper half of the main stem; 4 = lesions and/or gum exudation in the lower half of the main stem; 5 = tree dead.

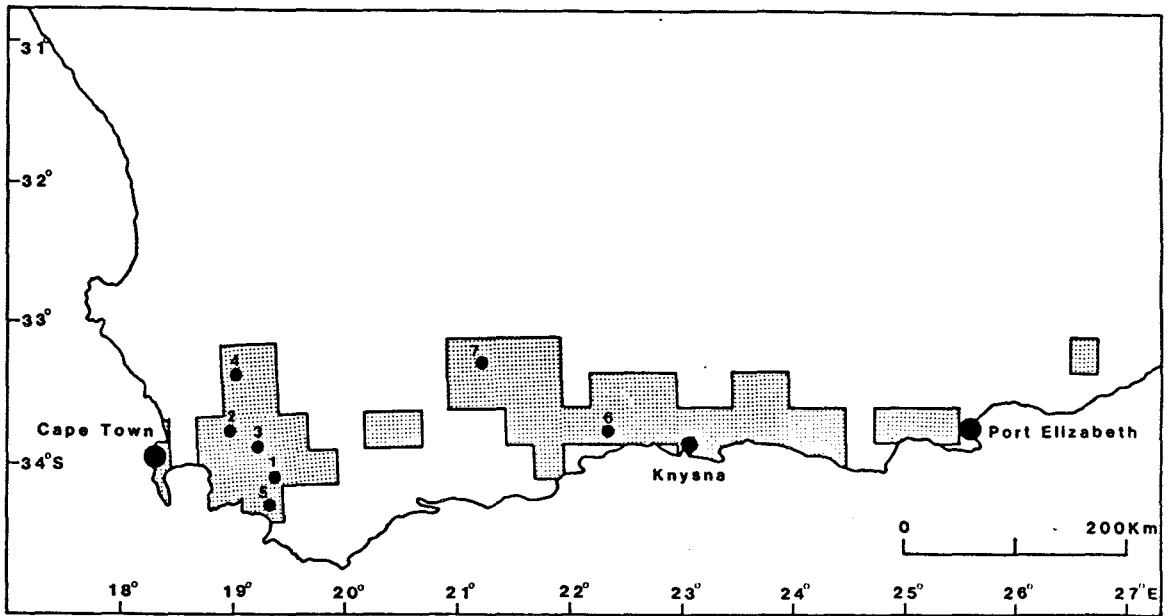


Fig. 17. The distribution of *H. sericea* in South Africa (shaded areas) showing the location of the seven *C. autologa* release sites used to evaluate the release method. Release sites and map coordinates are given in Table 13.

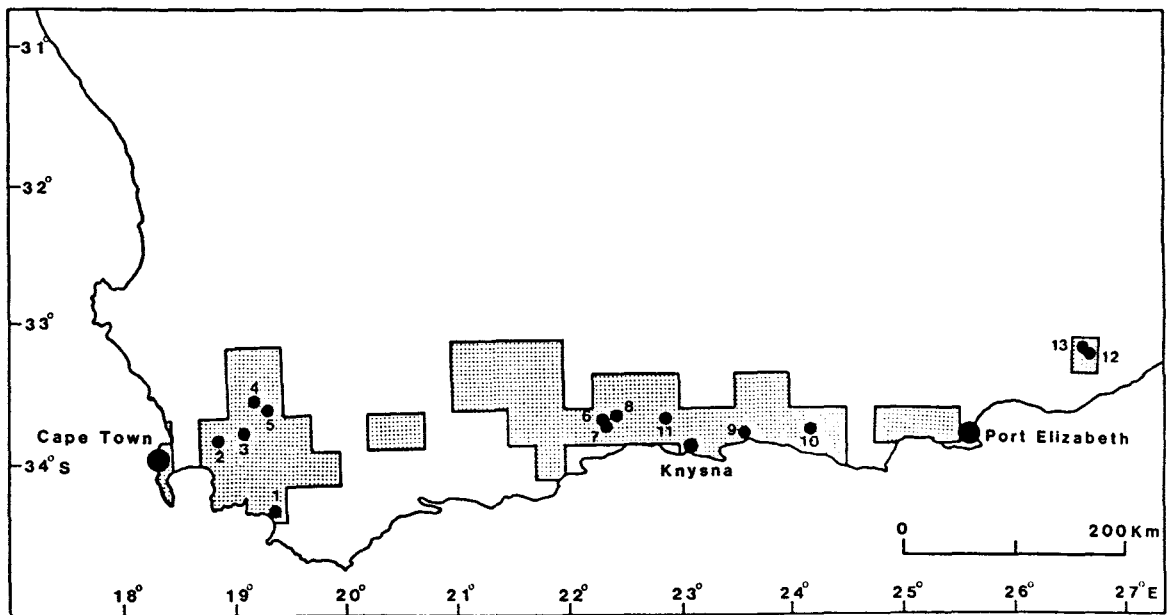


Fig. 18. The distribution of *H. sericea* in South Africa (shaded areas) showing the location of potential *C. autologa* release sites surveyed for *C. gloeosporioides*. Site details and map coordinates are given in Table 18.

Redistribution and establishment of *C. autologa* throughout the South African range of *H. sericea*

The redistribution of *C. autologa* was only initiated after the completion of the evaluation studies on the efficacy of *C. autologa* (Chapter 2). The reason being that large-scale harvesting of *C. autologa* for redistribution would adversely affect these studies, and secondly, the success of *C. autologa* as a biocontrol agent could only be fully determined after completion of these studies. Release sites were carefully selected to ensure that they were in areas of low fire risk, available for a number of years and that the incidence of fungus on the plants was low.

C. autologa releases were made in 1991 and 1992 and evaluated the year following release to determine whether *C. autologa* had successfully emerged from the fruits. These assessments were only done once all the larvae had emerged from the fruits. Samples of release fruits were collected and returned to the laboratory and inspected for signs of emergence holes or attempted entries. Fruits in the vicinity of the release fruits were also inspected for signs of emergence holes. When emergence holes were discovered in fruits in the vicinity of the release fruit, the distance between these fruits and the nearest release fruit were measured to obtain an indication of the distance the larvae can travel from the release fruit and successfully enter another fruit.

Cost of collecting and redistributing *C. autologa*

Since future costs of redistributing *C. autologa* will have to be borne by individuals or agencies who want to procure *C. autologa*, the costs using the above technique were determined. Only the costs of the physical collecting and processing of fruits were evaluated. This did not include transport costs or the time spent travelling to and from the sites.

RESULTS

Evaluation of the release method

The method of attaching egg-bearing follicles to healthy *H. sericea* fruits in the field yielded variable results. At Caledon, Villiersdorp, Paarl and Wolseley, between 20% and 23% of the release fruits yielded live larvae. At Hermanus and Burnsleigh (A) 14% and 11% of the fruits yielded live larvae. At Ladismith a mere 2% of the fruits were found with live larvae (Table 13).

The number of larvae that were unsuccessful in their attempts at entering the fruits varied between 2% at Ladismith and 9% at Villiersdorp (Table 13). The low number of unsuccessful entry attempts at Ladismith clearly indicates that the larvae did not die attempting to enter the fruits. It is suspected they moved off the fruits, perhaps because the *H. sericea* trees at Ladismith were young with abnormally small fruits at the time of release.

Although the overall success rate of attaching egg-bearing follicles appears to be low, it must be borne in mind that each follicle had one egg and that only 13.1% and 13.0% of the larvae were found to successfully complete their development within the fruits in South Africa (Chapter 3) and Australia (Neser, 1968), respectively.

This study showed that this method of release might prove to be a viable alternative to previously used methods, and it was decided to use it to redistribute *C. autologa* throughout the South African range of *H. sericea*.

Table 13. The percentage successful and unsuccessful entry attempts by *C. autologa* larvae at 7 release sites in the south-western and southern Cape.

Site no.	Locality (map co-ordinates)	Successful entries		Unsuccessful entries
		Larva alive	Larva dead or missing	
1	Caledon (34°13'S;19°28'E)	23	1	8
2	Paarl (33°50'S;19°01'E)	20	2	5
3	Villiersdorp (33°59'S;19°16'E)	21	2	9
4	Wolseley (33°29'S;19°09'E)	20	1	5
5	Hermanus (34°25'S;19°26'E)	14	4	5
6	Burnsleigh (A) (33°51'S;22°25'E)	11	4	5
7	Ladismith (33°30'S;21°16'E)	2	2	2

The incidence of fungus at potential release sites

Fungus was found at all the sites sampled except for one site at Grahamstown where no trace of the fungus was found (Fig. 19a). The eastern Cape region was found to have the lowest incidence of fungus (Fig. 19a) compared to the other two regions. However, the *H. sericea* infestations in the eastern Cape are not extensive and are restricted to Grahamstown and Port Elizabeth. In addition the *H. sericea* population that occurs in the Grahamstown area is reported to be different to the form that occurs between Port Elizabeth and Cape Town (Kluge, 1983).

In the southern Cape the incidence of fungus varied considerably from site to site. At Molen River 5.0% of the sampled trees had died due to fungus (Fig. 19e). A further 67.5% of the trees had lesions and/or gum exudation in the lower half of the main stem (Fig. 19d). Trees infected with fungus on the lower half of the main stem (class 4) rarely recover and the chances of them dying is very high (Chapter 4). At this site a mere 7.5% of the trees were healthy (Fig. 19a). This site would be totally unsuitable for *C. autologa* releases. At Waboomskraal (A), which has the largest trees and the most fruits (1458.2 fruits/tree; Table 18), 32.5% of the trees fell in class 4. Despite the presence of fungus, 65.0% of the trees were healthy and it was decided to release *C. autologa*, but on healthy trees only. At Burnsleigh (B), 90% of the trees were healthy and *C. autologa* was released at this site in 1992 (Table 14).

In the south-western Cape, fungus was prevalent at all sites sampled. The worst incidence of fungus was found at Jonkershoek and Franschhoek, however *C. autologa* has already

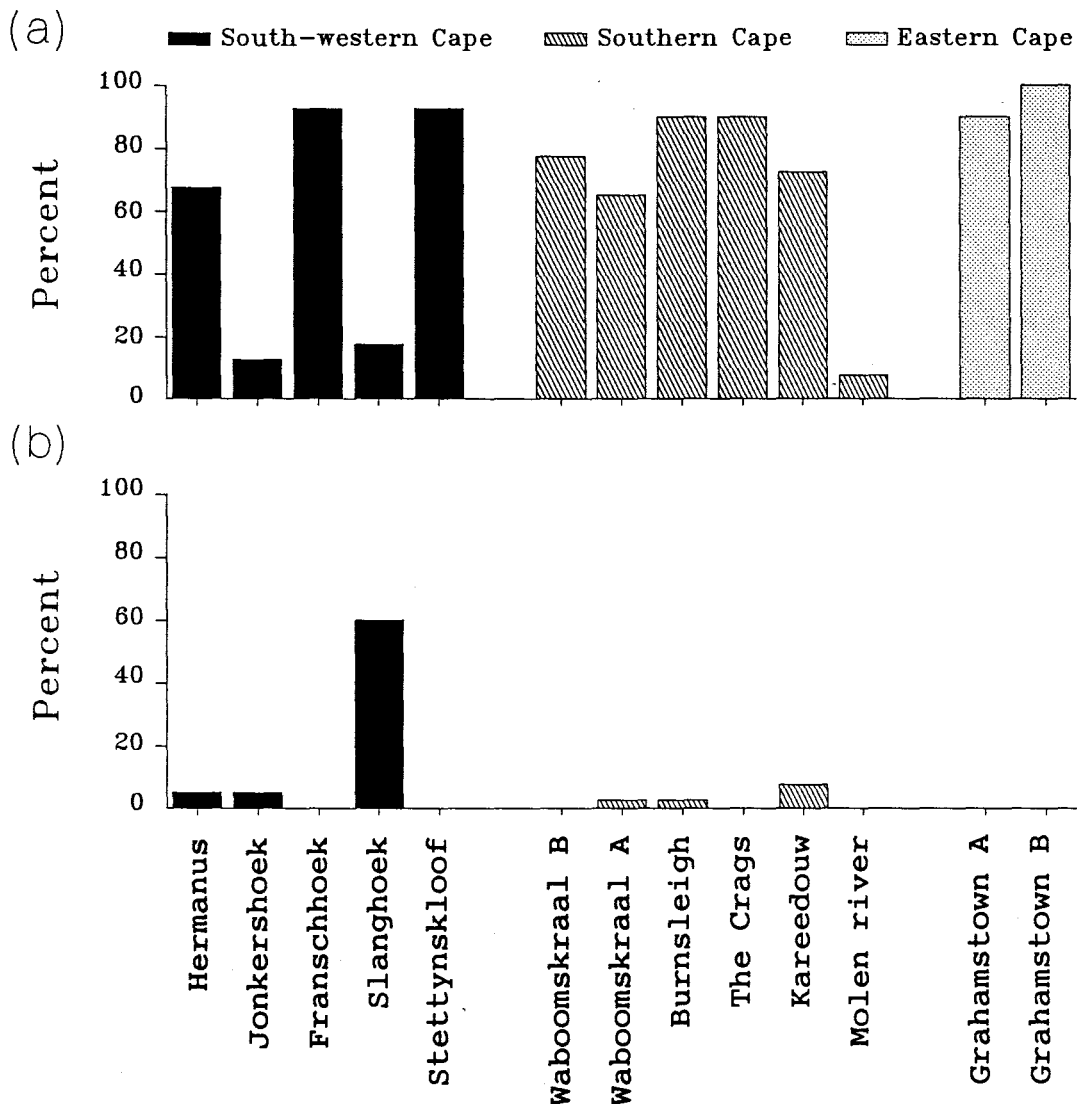


Fig. 19a. The percentage of fungus-free *H. sericea* trees at potential *C. autologa* release sites (Class 1.).

Fig. 19b. The percentage of *H. sericea* trees with their branches infected with fungus (Class 2.) at potential *C. autologa* release sites.

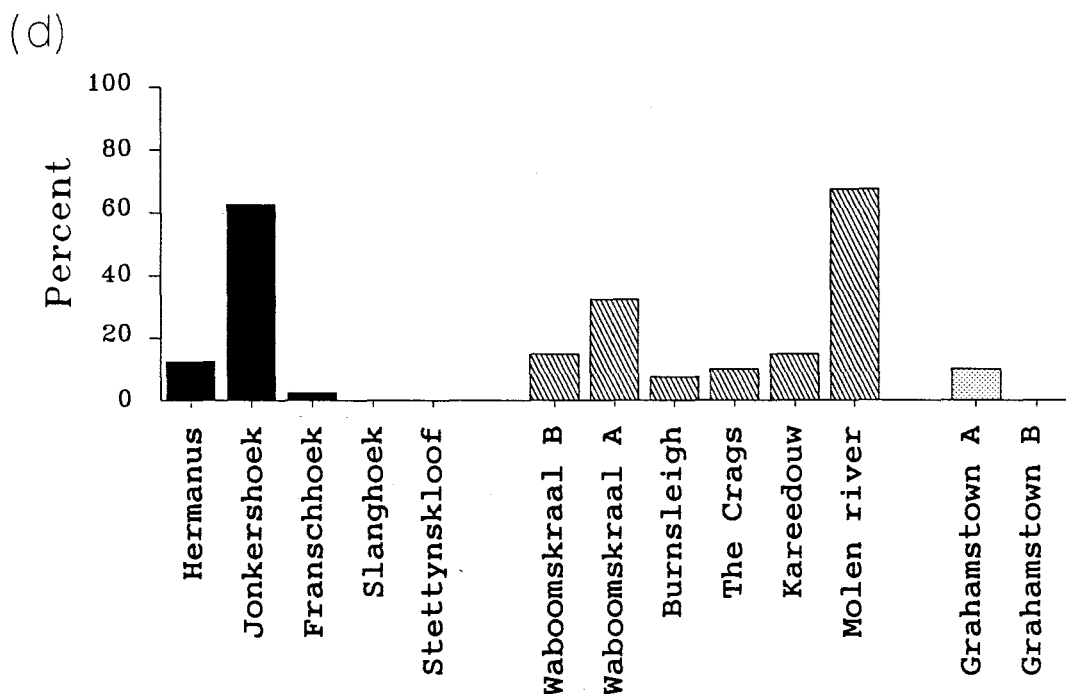
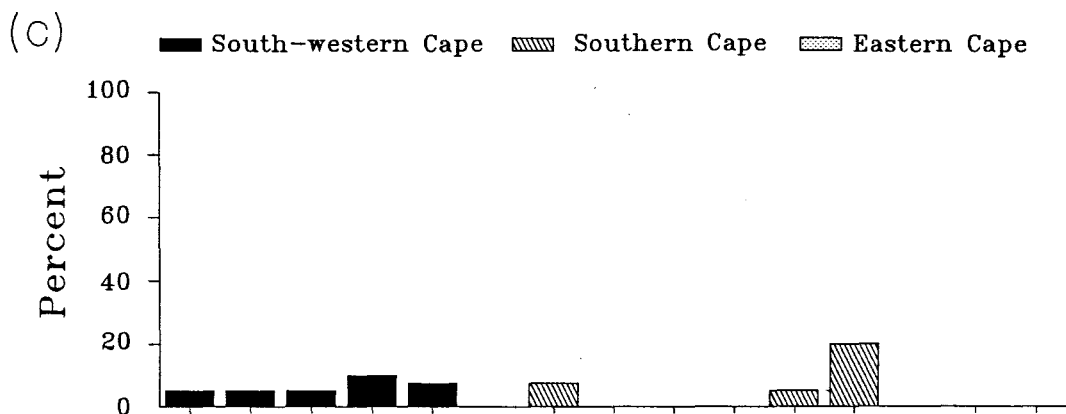


Fig. 19c. The percentage of *H. sericea* trees with fungus on the upper half of the main stem (Class 3.) at potential *C. autologa* release sites.

Fig. 19d. The percentage of *H. sericea* trees with fungus on the lower half of the main stem (Class 4.) at potential *C. autologa* release sites.

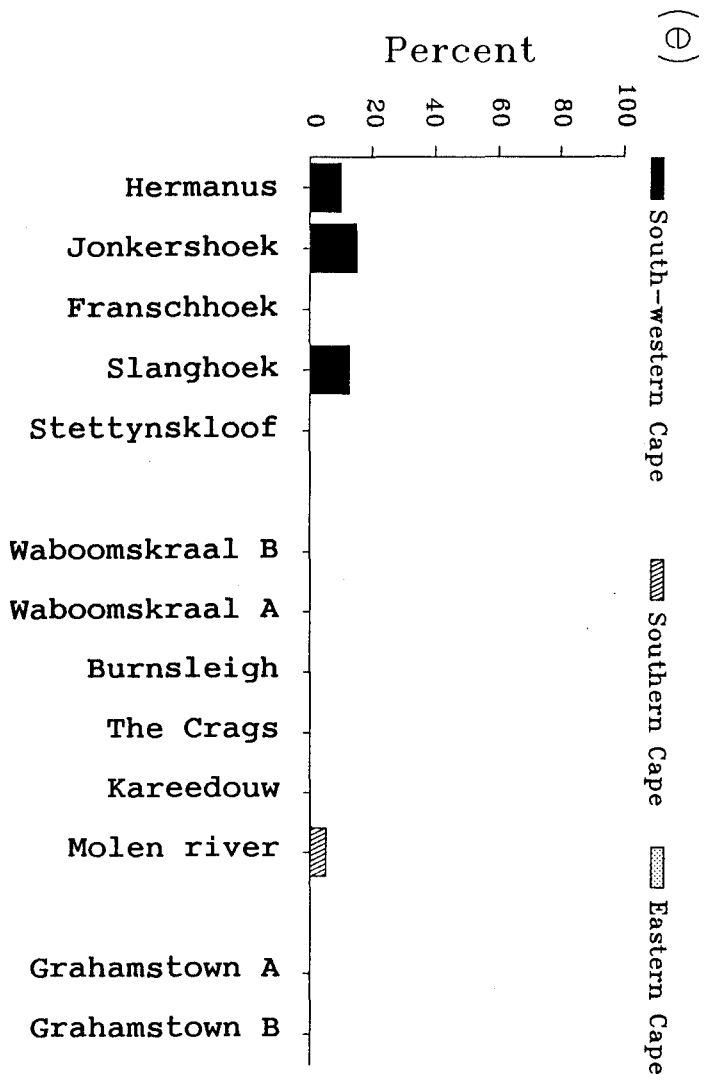


Fig. 19e. The percentage of *H. sericea* trees that have died due to fungus (Class 5.) at potential *C. autologa* release sites.

dispersed to both sites from neighbouring release sites (Chapter 2).

Redistribution and establishment of *C. autologa* throughout the South African range of *H. sericea*

Although it was initially planned to redistribute *C. autologa* to as many sites as possible, it became clear that this would not be feasible. The reason being that large-scale harvesting of eggs would deplete the *C. autologa* populations at Paradyskloof; between 2500 and 3000 fruits are required to yield enough eggs per site. Therefore only 3 releases per annum were made. Seven releases were made

Table 14. Date, locality, map co-ordinates and number of egg-bearing follicles attached to healthy fruit at each site.

Site no.	Release date	Locality	Map co-ordinates	No. follicles attached
1	June 1990	Burnsleigh (A)	33°51'S;22°25'E	753
	June 1991			328
2	June 1991	Waboomskraal (B)	33°51'S;22°21'E	1403
3	June 1991	Caledon	34°13'S;19°25'E	767
4	May 1992	Burnsleigh (B)	33°50'S;22°26'E	759
5	May 1992	Joubertina	33°49'S;23°48'E	700
6	June 1992	Steenboksberg	33°31'S;19°07'E	635

between 1990 and 1992 at a number of sites in the southern and south-western Cape (Table 14; Fig. 20). The number of eggs per follicle were not recorded, but varied between one and nine eggs.

The releases made in 1990 and 1991 (Table 14) were evaluated the year following release. The percentage of fruits with emergence holes were 30.3%, 33.4% and 6% for Burnsleigh (A), Caledon and Waboomskraal (B), respectively (Table 15). These figures include emergence holes both in release fruits and in fruits in the vicinity of the release fruits. The fruits in the vicinity of release fruits were inspected for emergence holes because the larvae are known to move off the fruits (Chapter 3).

At the above three sites (Burnsleigh (A), Waboomskraal (B) and Caledon), 14.0, 19.2 and 14.9% of the fruits with emergence holes, respectively, were found in the vicinity of release fruits. The maximum distance that a neonate larva

Table 15. The number of release fruits sampled at three release sites and the percentage thereof with emergence holes (includes healthy fruits in the vicinity of release fruits with emergence holes).

Release site	Year released	No. of release fruits sampled	% fruits with emergence holes
Burnsleigh (A)	1990	188	30.3
Waboomskraal (B)	1991	430	6.0
Caledon	1991	722	33.4

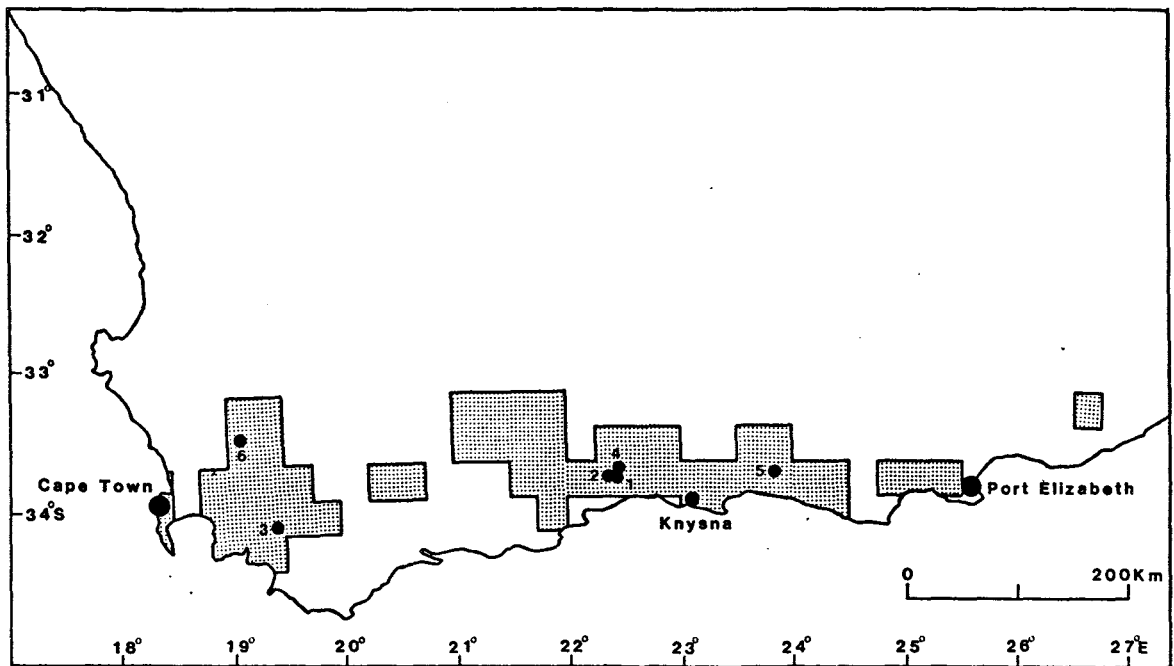


Fig. 20. The distribution of *H. sericea* in South Africa (shaded areas) showing the location of the *C. autologa* releases made from 1990-1992. Site details and map co-ordinates are given in Table 14.

moved from a release fruit and successfully entered and completed its development within another fruit, was 17cm. The average distance recorded was 7cm.

The percentage of fruits with emergence holes was considerably higher than initially expected *i.e.* higher than the pilot study. This is probably because the follicles used in that study had one egg per follicle, whereas many of the follicles used for large-scale releases had more than one egg.

The percentage of fruits with emergence holes at Waboomskraal (B) was a disappointing 6% compared to the 30.3% at Burnsleigh (A) and the 33.4% recorded at Caledon (Table 15.) The egg-bearing follicles used for the Waboomskraal (B) and Caledon release were collected at the same time and released over the same period and it is therefore unlikely that this influenced the poor returns obtained at Waboomskraal (B).

To determine whether climatic conditions might not have contributed to the poor results, the average daily maximum temperatures (Fig. 20a) and daily rainfall (Fig. 20b) for June, July and August 1991 and 1992 were compared for Oudtshoorn, the nearest weather station to Burnsleigh (A) and Waboomskraal (B). These comparisons show no noticeable difference in the prevailing weather conditions during the crucial stage prior to the larvae safely entering the fruits (Fig. 20a & 4b).

C. autologa was introduced from southern and south-eastern New South Wales, Australia. These two regions have mediterranean- and temperate-type climates, respectively

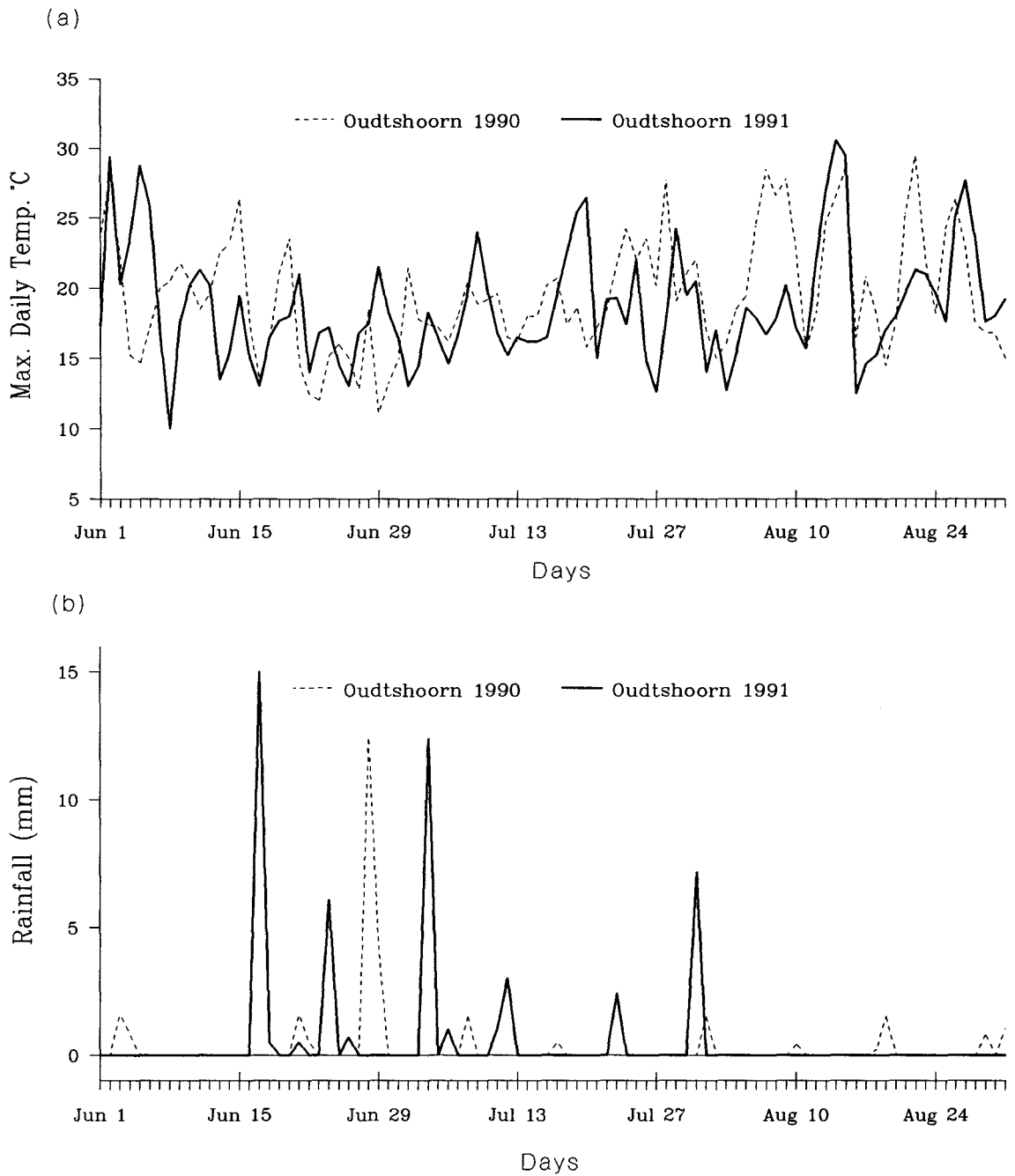


Fig. 20. A comparison of the maximum daily temperature (a) and daily rainfall (b) for the months June - August for Oudtshoorn 1990 and 1991.

which are similar to the climatic conditions in those parts of South Africa in which *H. sericea* occurs.

To determine whether the dry hot summers experienced in these regions might not be unsuitable for some development stages within the fruits, the release fruits from Waboomskraal (B) and Caledon were opened. The number of unsuccessful entry attempts and any larval mortality within the fruits were recorded. The percentage of fruits where the larvae had died after one or both seeds had been eaten did not differ noticeably, and in fact larval mortality within the fruits was higher at Caledon than Waboomskraal (B) (Table 16).

Table 16. The percentage of fruits with emergence holes and with one or both seeds consumed by *C. autologa* larvae at Waboomskraal (B) and Caledon.

Site	No. fruits sampled	% with emergence holes	% fruits with one or both seeds eaten	% attempted entries
Waboomskraal (B)	430	6.0	0.7	7.2
Caledon	722	33.4	5.4	5.1

Assessment of the costs required to collect and redistribute
C. autologa

It is estimated that approximately 750 egg-bearing follicles are required per site to start a viable field colony. This would mean that between 2500 and 3000 fruits would have to be collected in the field to yield this number. This would take between 8 and 9 man/hours (Table 17). The inspection and splitting of the fruits takes an additional 8 to 9 man/hours (Table 17). These processes are fairly simple and can be performed by unskilled labour who work at a present rate of R18/hour. This part of the operation will therefore cost in the vicinity of R300.

Table 17. The number of *H. sericea* fruits collected at Paradyskloof during 1992 and the number with eggs, including the man/hours to collect and process the fruits for release.

Date	No. fruits collected	No. (%) fruits with eggs	Collecting man/hours	Processing man/hours
11.5.92	2919	802 (27.5)	10.5	9
13.5.92	2299	657 (28.6)	9	8
09.6.92	2404	635 (26.4)	9	8.5

The method of attaching egg-bearing follicles to healthy fruit in the field is extremely quick, depending on how exposed the fruits are on the trees. Invariably the fruits on older trees are more exposed than the fruit on younger trees. At Burnsleigh (B) 759 egg-bearing follicles were attached to healthy fruits in 2 hours. The trees at Burnsleigh (B) are older with many fruits. At Steenboksberg 635 egg-bearing follicles were attached to healthy fruits in 3 hours. The difference in time taken between the different sites is attributed to the fact that the fruits on the older trees at Burnsleigh (B) are more exposed than the fruits on the younger trees at Steenboksberg. This part of the operation will therefore cost in the vicinity of R60.

DISCUSSION

The alternative release method developed for the redistribution of *C. autologa* was shown to be efficient and not as time consuming or labour intensive as the "drilling" method used previously. The number of larvae that successfully emerged from both the release fruits and from fruits in the vicinity of the release fruits at Burnsleigh (30.3%) and Caledon (33.4%) was most surprising. Naser (1968) found that only 13% of the larvae successfully completed their development in Australia, and at Paradyskloof only 13.1% of the fruits with eggs yielded mature larvae (Chapter 3). Many of the egg-bearing follicles attached to healthy fruit in the field had more than one egg, which might have improved the chances of success *i.e.* compensated for larvae that moved off the fruits.

If one extrapolates from the results of the samples taken at Burnsleigh (A), Waboomskraal (B) and Caledon then approximately 228, 84 and 256 larvae successfully emerged from the fruits at each site, respectively. This should be sufficient to start a viable colony at both Burnsleigh (A) and Caledon. At Knorhoek, where larvae were inserted into 574 fruits using the drilling technique in 1981, 279 larvae successfully emerged from these fruits the year following release and successfully established a viable colony (A.J. Gordon, unpublished results, 1982).

The low success rate found at Waboomskraal (B) is disconcerting. This site consists of large trees with huge seed stores and was considered an ideal site for *C. autologa*. It is unlikely that the quality of the eggs or the weather conditions contributed to the poor establishment. It is suspected that the quality of the fruits might have influenced the larvae. The egg-bearing follicles were attached to older fruits on the lower half of the trees because the younger fruits were out of reach at the top of the trees. The very old fruit tend to split open slightly along the suture and the larvae may not have found them suitable. If this is the case, it will limit the effectiveness of *C. autologa* and should be investigated.

Although the fungus is wide spread, it has not reached epidemic proportions in the areas surveyed, with the possible exception of Jonkershoek, Franschoek and Molen River. *C. autologa* has, however, established at Jonkershoek and Franschoek despite the high incidence of fungus. Releases can therefore be made throughout the South African range of the weed. The ability of the moth to spread at low infestation levels will undoubtedly mean that fewer releases need be made in a specific area. It is however important to

get *C. autologa* established in the eastern Cape and at more sites in the southern Cape, before spreading it widely in the south-western Cape. It is recommended that releases be made at Stettynskloof, Grahamstown and The Craggs as soon as possible and that further releases be made at Waboomskraal to supplement the 1991 release.

Large-scale releases of *C. autologa* are presently limited by the low population levels prevailing at present release sites. As soon as the populations have increased sufficiently then they too can be utilized for the harvesting of eggs.

To collect and process enough eggs for a single release costs approximately R300-R400, which is not considered excessive. As most of the eggs are oviposited in protected positions on the fruits, and the method of release so simple, egg-bearing follicles can be posted to interested parties for release.

Table 18. The locality (map co-ordinates) and average height, stem circumference and number of fruits per tree at selected, potential *C. autologa* release sites.

Site no.	Locality (co-ordinates)	Height (m)	Stem circumference (mm)	Mean no. of fruits per tree
South-western Cape				
1	Hermanus (34°25'S;19°27'E)	2.8	153.4	371.0
2	Jonkershoek (33°58'S;18°54'E)	4.1	231.7	712.1
3	Franschhoek (33°55'S;19°08'E)	2.6	72.7	17.6
4	Slanghoek (33°40'S;19°14'E)	2.9	98.5	70.7
5	Stettynskloof (33°48'S;19°18'E)	1.2	32.5	12.9
Southern Cape				
6	Waboomskraal (A) (33°50'S;22°21'E)	3.8	244.6	1458.2
7	Waboomskraal (B) (33°51'S;22°21'E)	2.9	121.3	18.8
8	Burnsleigh (B) (33°50'S;22°26'E)	3.3	126.8	131.1
9	The Craggs (33°56'S;23°34'E)	3.3	137.5	41.8
10	Kareedouw (33°55'S;24°11'E)	1.9	90.0	19.0
11	Molen River (33°48'S;22°51'E)	2.6	119.4	41.3
Eastern Cape				
12	Grahamstown (A) (33°20'S;26°38'E)	3.4	132.0	105.8
13	Grahamstown (B) (33°20'S;26°36'E)	2.8	175.5	178.1

CHAPTER 7

An overview of the role of *C. autologa* in the *H. sericea* biological control programme

A number of studies have been undertaken to determine the degree of predispersal seed predation of annuals and short-lived perennials (Lamp & McCarty, 1982; Forsyth & Watson, 1985; Story *et al.*, 1991), and woody perennials (Louda, 1982a,b, 1983; Auld, 1986; Auld & Myerscough, 1986; Andersen, 1989b). The potential of seed predators to reduce recruitment has often been doubted (Wilson, 1949,1964; Huffaker, 1957,1964; Holloway, 1964; Harris, 1973; Goeden, 1983; Janzen, 1986; Andersen, 1989a). It is especially in the case of perennial weeds where the suitability of seed predators is questioned (Huffaker, 1957). The justification for this school of thought is that perennials do not need to reproduce in every season and have less need for seed production. However, recent research has shown that reduced seed production might contribute to a reduction in the density and rate of spread of some weeds (Louda, 1982a; Neser & Kluge, 1986; Hoffmann, 1990; Hoffmann & Moran, 1992).

Predispersal seed predation on its own is often not enough to suppress a weed and it is often a combination with other factors such as post-dispersal seed predation, the lack of 'safe sites' (see below), seedling mortality etc that contributes to final control. Predispersal seed predation of *Cirsium arvense* (L.) Scop. by *Orellia ruficauda* (Fabr.) was not considered severe, but combined with various characteristics of the weed (low seed germination and low

seedling survival) it may have been an important factor in reducing the spread of the weed (Forsyth & Watson, 1985). Duggan (1985) on the other hand found that pre-dispersal seed predation of *Cardamine pratensis* L. was high, but did not greatly affect the dynamics because recruitment from seed is infrequent and is limited by microsite availability.

In this final chapter the following will be discussed, (a) the impact of *C. autologa* on the density and dispersal of *H. sericea*, (b) features of *C. autologa* and *H. sericea* that have influenced the success of this project, (c) the role of *C. autologa* in the biological and integrated control of *H. sericea* programmes and finally (d) can *C. autologa* be classified as a biological control success?

The effect of *C. autologa* on the density of *H. sericea*

It is one thing to show that herbivorous insects affect plant performance, but it is an entirely different matter to demonstrate that insect herbivory affects plant population dynamics (Crawley, 1989a). The level of pre-dispersal mortality required to reduce the density and spread of *H. sericea* is extremely difficult to predict. Seed predation will only act to control the population if it reduces the seed density below that to which it would be reduced in any case by density-dependant mortality (Fenner, 1985).

There are examples of insects reducing the density of weeds. At a study site at Goudini in the south-western Cape, the annual *H. sericea* fruit loss increased from 39% in 1979 to 81% in 1981, mainly as a result of *E. consputa* activity

(Neser & Kluge, 1985). A wild-fire swept through this site in 1982 and two years later the density of *H. sericea* seedlings was found to be only 10% that of the pre-fire density of parent plants (Neser & Kluge, 1986). Predispersal predation markedly affected the population recruitment and abundance of the shrub *Haplopappus squarrosus* H. & A. in the next generation (Louda, 1982a). Alternatively, the biocontrol agents *Urophora quadrifasciata* (Meigen), *Urophora affinis* (Frauaenfeld) and *Metzeneria paucipunctella* Zeller reduced seed production of diffuse knapweed, *Centaurea diffusa* (De Lamarck), by 80-95% but had no effect on knapweed density (Müller & Schroeder, 1989)

It is not only seed predation that can limit population recruitment. Successful regeneration by a plant also depends on the frequency of 'safe sites'. 'Safe sites' provide the precise conditions required by a particular seed to germinate (Harper *et al.*, 1965). A 'safe site' is also a site free of specific hazards such as predators, competitors, toxic soil constituents and pre-emergence pathogens (Harper, 1977). Diurnal rodents are known to consume large quantities of *H. sericea* seed beneath felled *H. sericea* trees (Richardson, 1985).

At the end of 1990, the mean seed reduction achieved by *C. autologa* at Paradyskloof and Knorhoek was 64.2% and 50.6%, respectively. Whether this level of seed predation will significantly reduce the recruitment of seedlings below the density of the parent plants is not known. It will only be possible to quantify any reduction in the density of *H. sericea* at the study sites after a fire. With fewer seeds being released after a fire, the effect of the serotinous strategy of *H. sericea* will be considerably diminished. The density of the new generation of *H. sericea*

seedlings can then be compared to the density of the parent population.

The effect of *C. autologa* on the dispersal of *H. sericea*

Predispersal mortality will also affect the dispersal of *H. sericea* seeds. A reduction of 50% of the seed crop will halve the number of seeds reaching any point in the dispersal range, and will alter the distance from the seed crop at which any particular density of seeds will land (Harper, 1977). The winged seeds of *Hakea* species facilitate dispersal over several kilometers (Richardson *et al.*, 1987). *C. autologa* has reduced the accumulated seed store at Paradyskloof and Knorhoek by at least 50% (Chapter 2; Gordon, 1993 in press; Appendix 1) and will therefore contribute to a reduction in the potential rate of spread. A reduction in the number of seeds being dispersed will result in the formation of fewer nascent foci. Satellite foci can become the paramount problem for eventual weed control, even when the main infestation is allowed to grow unimpeded (Moody & Mack, 1988). Fugler (1982) has recommended that outlying populations of *H. sericea* should be destroyed first before methodically reducing the area of the main infestation.

Richardson *et al.* (1987) contribute the invasiveness of *H. sericea* relative to other *Hakea* species to the production of large numbers of viable seeds. For example, the average seed loads on a shrub with a dry mass of 14kg range from 100 on *H. drupacea* (= *H. suaveolens*) to about 500 on *H. gibbosa* and 2000 on *H. sericea* (Kruger *et al.*, 1986). The invasiveness of *H. sericea* will be greatly reduced if the

seed load can be reduced to the same level as *H. drupacea* and *H. gibbosa*.

Features of *H. sericea* and *C. autologa* influencing the success of the biological control programme

Features of *Hakea sericea*

There are several possible means which plants employ to reduce seed loss to predispersal predators. In addition to mechanical and chemical defenses there is the phenomenon of "mast" years. Mast years are particularly strongly developed in woody perennials (Harper, 1977). In a mast year the seed production is very high and is followed by a number of years in which relatively few seeds are produced. The predator populations are unable to adjust quickly enough and are thus alternately satiated and starved. In mast years a significant proportion of seeds escape predation. Fluctuating fruit crops of witch-hazel *Hamamelis virginiana* L. are responsible for limiting *Pseudanthonomus hamamelidis* Pierce numbers during poor fruiting years (De Steven, 1981). The simultaneous release of canopy-stored seed by some species may be analogous to mast fruiting and be a means of escaping seed predation (Gill, 1981). The strategy behind mass seed release is to enable as many seeds as possible to escape predation, resulting in major seedling recruitment. *C. autologa* can neutralize this phenomenon by reducing the seed source.

C. autologa is a predispersal seed predator and therefore these strategies will not influence its effectiveness.

Furthermore, *C. autologa* attacks the mature seeds, and once seeds mature, their death cannot be perceived by the parent (Janzen, 1971). The host plant therefore cannot actively compensate for increased predation of the mature seeds. Therefore, not only is *H. sericea* unable to compensate for seed loss due to *C. autologa*, but the seeds are retained on the plant and are available as a continuous source of food.

No variable fruiting has been detected in *H. sericea* (Kluge, 1983) and no large fluctuations in the quantity of seed added to the canopy have been recorded in the present study. Fluctuations in the *E. consputa* populations will cause fluctuations in the number of immature seeds escaping attack and being added to the seed store. However, it is suspected that *E. consputa* will maintain a consistent level of attack over a long period of time (Kluge, 1983). *C. autologa* populations are not expected to fluctuate since there will always be sufficient fruits to maintain the population.

Features of *C. autologa*

Normally the best method used to evaluate the impact of an insect herbivore on a plant population are insect exclusion experiments (Wapshere 1982; Crawley, 1989a). Recent exclusion studies which quantify predispersal seed predation are those of Green & Palmbald (1975) and Louda, (1982a,b). In the case of *C. autologa* this was not necessary because (a) the fruits are retained on the trees before and after attack and (b) the emergence hole is clearly visible indicating successful attack. Assessing pre-dispersal seed losses based on observations of mature fruits has been

questioned by Janzen (1971) and shown to be unreliable by Andersen (1988). However, in the present study the fruits were opened at the end of the study period to determine the fate of seeds inside the fruits.

Herbivores seldom increase sufficiently in number to destroy their host plant populations and their food resources (Pimental, 1961;1988). However, in the case of *C. autologa*, there is no "restriction" on their numbers since there is no possibility of them destroying their host: there will always be one seed crop available to them (Chapter 5). Once the back-log of accumulated fruits has been largely depleted by *C. autologa*, then only the annual seed crop will remain. Moths will however, continue to lay on both new and old fruits and relatively few fruits will escape predation. The longer a fruit remains on the tree, the greater the chance of it being attacked.

There have been many reported cases of predators, parasitoids and pathogens influencing the outcome of biological control of weeds projects (Goeden & Louda, 1976). In South Africa, the biocontrol agent, *Zeuxidiplosis giardi* Kieffer was contributing to the control of *Hypericum perforatum* L. (Gordon *et al.*, 1985; Gordon & Neser, 1986). However, it is suspected that indigenous parasitoids are responsible for its subsequent reduced effectiveness (Gordon & Kluge, 1991). Natural enemies play an important role in limiting herbivore numbers, but no parasites were found attacking *C. autologa*.

Carposina autologa has shown that it is capable of dispersing at low population levels, however its ability to find and establish on isolated or scattered plants remains to be seen. Despite certain aspects of its phenology which

will obviously limit the population growth of *C. autologa*, i.e. the inability of the moths to distinguish between healthy and attacked fruits and the high pre-penetration mortality, the moth has performed surprisingly well. The high larval mortality found in South Africa (Chapter 3) and in Australia (Neser, 1968) need not necessarily have an adverse effect on the success of *C. autologa* as a biocontrol agent. The average pre-adult mortality of *Bangasternus fausti* Reitter, a potential biological control agent of diffuse knapweed, was found to be 95.8%, yet a one-hundred percent seed destruction was recorded in 18.7% of 502 field collected seedheads (Sobhian *et al.*, 1992)

There have been 499 releases of exotic invertebrate organisms and fungi against 101 weed species (Julien *et al.*, 1984). In only 29% of all releases were the agents effective. The Carposonidae have a poor record in biocontrol of weeds programmes. There have been 7 incidences where they have been used. In all these cases they established but control was at best only slight (Crawley, 1989b).

The high level of inherent homeostasis that exists between *C. autologa* and *H. sericea* may have limited its efficacy as a successful biological control agent. Dennill and Hokkanen (1990) have emphasized that the achievement of success in biocontrol is dependant on both the release of an agent from its natural enemies, and the degree of homeostasis in the relationship between the host and the agent. Despite being released from its natural enemies, *C. autologa* will not be able to fully exploit *H. sericea* (Chapter 5).

The role of *C. autologa* in the biocontrol of *H. sericea* programme

Biological control can seldom be achieved by a single organism, especially where several different environments are invaded by the pest (Haseler, 1980). Most weeds probably require three or more natural enemies to achieve control (Forsyth & Watson, 1985). There are examples in biological weed control where one agent has been responsible for spectacular success in the control of a weed, for example, *Chrysolina quadrigemina* Suffrain on *Hypericum perforatum* in California (Huffaker & Kennett, 1959), but this is rare. It is beneficial to establish as many agents as possible, but care should be taken that they do not compete with those already introduced. Story *et al.* (1991) suggest the establishment of as many exploitive competitors (those that indirectly affect their neighbors due to the reduction of resources) as possible. *C. autologa* on its own might not be considered a severe predator, however, when combined with *E. consputa* it might be an important factor in reducing the density and spread of *H. sericea*. The combined damage caused by *Trichapion lativentre* (Beguin Billecocq) (98% reduction in seed-set) and the seed-feeding curculionid, *Rhyssomatus marginatus* Fåhraeus (98% reduction in remaining seeds) reduces the reproductive potential of the perennial leguminous weed, *Sesbania punicea* by 99.8% in South Africa (Hoffmann & Moran, 1992).

The combined attack of *C. autologa* and *E. consputa* should be sufficient to control *H. sericea*; however, if an additional insect is considered then it should be one that is compatible with the two already released. A likely candidate is the bud feeding weevil, *Dicomada rufa*

Blackburn. This insect is almost certainly specific (Kluge & Nesar, 1991) and could prove to be a valuable supplement to both *C. autologa* and *E. consputa*. An added advantage is that it disperses rapidly, and will be able to quickly reinfest areas after fires (Kluge & Nesar, 1991).

The role of *C. autologa* in an integrated control programme

An integrated control programme for *H. sericea* has been implemented in South Africa (Kluge *et al.*, 1986). The Department of Forestry have an active mechanical clearing program in mountain catchment areas. It was predicted that the proclaimed mountain catchment areas in the south-western Cape would be reduced to isolated areas of scattered, and medium density infestations by 1990 (Fenn, 1980), however wild-fires and budgetary constraints have severely hampered the programme. In the present economic climate money for conservation is in short supply. The City Council of Cape Town has put the cost of clearing alien vegetation at R1585 per hectare (R978 in labour, R245 in transport and R362 in materials such as herbicides, petrol and oil).

Large areas have been cleared of *H. sericea* on State Forest land by the Department of Forestry, but if control measures are not maintained infestations can easily revert to their previous levels. An additional problem is *H. sericea* infestations on private, non-mountain catchment land. It is feared that these infestations will be a source of reinfestation. The Department of Forestry have no authority to clear this land nor do the land owners have the resources.

Recent research has shown that the slash and burn techniques used by the Forestry department, which result in intense fires, have a detrimental effect on the ecosystem (Richardson & van Wilgen, 1986; Breytenbach, 1989). This has led to a call for alternative control procedures (Breytenbach, 1989), or that fire behaviour prediction models be used when felled hakea is burned in order that burning takes place under conditions that will lead to less intense fires (Richardson & van Wilgen, 1986).

A number of herbicides have been registered for *H. sericea* and *H. gibbosa* (Kluge *et al.*, 1987; Donald & Nel, 1989; Vermeulen & Rankin, 1990). However, chemical control of *H. sericea* and *H. gibbosa* is an expensive control method (Donald & Nel, 1989) and can have a detrimental effect on the indigenous vegetation (Taylor, 1969; Fenn, 1980).

A method of controlling young seedlings using a wheat bran formulation of *C. gloeosporioides* has been developed (Morris, 1989). The mean percentage seedling mortality in trials using this method was between 30% and 98% (Morris, 1989). Trials to determine the value of introducing the fungus into strips of maturing plants are currently being done by the Cape Provincial Nature Conservation Department (Morris, 1991). This method of control is unfortunately not compatible with *C. autologa* (see Chapter 4), however many landowners can ill afford the expense or the labour to apply it.

There is plenty of support for the biological control of hakea (Richardson *et al.*, 1987; Breytenbach, 1989). The biological control of *H. sericea* does not suffer from a conflict of interest situation which have affected other biocontrol programmes in South Africa (Dennill & Donnelly,

1991; Donnelly *et al.*, 1992) and will be the best long-term solution for the eventual control of *H. sericea*.

The redistribution of *C. autologa* is expected to be a slow process, since population levels are still comparatively low. Special care will have to be taken to ensure that the populations are not depleted at Paradyskloof. It will be a number of years before large-scale harvesting of eggs can take place at Knorhoek and the other recently established populations. Release sites will have to be carefully selected to improve the chances of establishment and should be made in areas where there is little or no incidence of fungus. The effect of the fungus, *C. gloeosporioides* on *C. autologa* populations at the two study sites has definitely contributed to the slow establishment and colonization of the moth (Chapter 4).

The fungus is not as devastating in the southern or eastern Cape where *H. sericea* is still a major problem. The climate in these areas differ from the climate in the south-western Cape and it is difficult to predict how effective the moth will be in these regions. The gall wasp *Trichilogaster acaciaelongifoliae* Froggatt was released throughout the distribution area of the weed *Acacia longifolia* (Andr.)Willd. in the Cape Province and Natal, South Africa. However, in the hotter inland valleys and the west coast of the south-western Cape Province, and in Natal, establishment was poor and infestation levels were consistently low (Dennill & Gordon, 1990). Release sites will also have to be established away from areas of human interference. Dennill (1987b) found that 9% of *Trichilogaster acaciaelongifoliae* release sites were totally destroyed by human interference. Due to the slow establishment and dispersal of *C. autologa*, release sites will be vulnerable

to both wild-fires and human interference for long periods of time.

The success of *C. autologa* as a biological control agent

Biological control practitioners have different interpretations for the definition of a successful biocontrol agent (Huffaker, 1957; Harris, 1981; Julien *et al.*, 1984; Wapshere, 1985). Dennill (1987b; 1990) suggests that success in biocontrol be defined in terms of the achievement of the particular aims specified. *Carposina autologa* was introduced to reduce the amount of accumulated seeds released after fires and in this sense has achieved the original aim. However, I feel that only once *C. autologa* has contributed to a reduction in the density and spread of *H. sericea* can it be classified a biocontrol success. To show this, however, will take many years.

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APPENDIX 1

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1

The impact of the Hakea seed-moth *Carposina autologa* (Carposinidae) on the canopy-stored seeds of the weed *Hakea sericea* (Proteaceae)

A.J. Gordon

Plant Protection Research Institute, Private Bag X5017, Stellenbosch 7600, South Africa

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ABSTRACT

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The Hakea seed-moth, *Carposina autologa* Meyrick was released in South Africa for the biological control of *Hakea sericea* Schrader. The impact of the moth on the canopy-stored seeds of *H. sericea* was evaluated in the southwestern Cape over 3 years. The moth has reduced the mean accumulated seeds at the two study sites by 64.2% and 50.6%. It has shown a surprising ability to disperse and establish new colonies at low population levels. Although seed destruction is not severe, it is expected to contribute to the control of the weed.

INTRODUCTION

Hakea sericea Schrader (silky hakea) is an erect, single-stemmed, branchy shrub which grows to a height of 2–5 m. It was introduced to South Africa from Australia during the 1930s. It has become a major problem in nearly all the coastal mountain ranges of the Cape Province (Neser and Fugler, 1978), where it often forms dense, impenetrable thickets and poses a serious threat to the floristically rich and unique mountain 'fynbos' (macchia). In 1983, almost 480 000 ha of mountain fynbos were affected to varying degrees (Kluge and Richardson, 1983).

Factors thought to have contributed to the success of *H. sericea* as an invader of South Africa, are its copious production of serotinous seeds, high seed longevity in the canopy and efficient seed dispersal. In dense, mature stands of *H. sericea*, seed densities of up to 7500 seeds m^{-2} (Kluge, 1983)

Correspondence to: A.J. Gordon, Plant Protection Research Institute, Private Bag X5017, Stellenbosch 7600, South Africa.

have been reported. The seeds, produced annually, are stored in the canopy and are only released after either a fire or the death of the plant. Fires are an important feature of the fynbos vegetation and are necessary for species survival (Van Wilgen, 1981; Van Wilgen and Richardson, 1985).

The fruit of *H. sericea* consists of a woody follicle comprising two dehiscent valves. Each valve contains one, black, winged seed. Each seed is 8 mm in length and 5 mm in width and has a membranous wing of length 15 mm and width 10 mm.

In order to reduce the number of seeds released after fires, two seed-feeding insects were introduced from Australia. The weevil, *Erytanna consputa* Pascoe (Curculionidae: Eirrhiniinae), which destroys the immature fruits of *H. sericea*, and whose adults feed on buds, flowers and young fruits, was released in 1972 (Neser and Annecke, 1973). *E. consputa* was the first biological control agent successfully established against *H. sericea* in South Africa. At a study site in the southwestern Cape, where 20 adults were released in 1975, fruit loss increased to 81%, 86% of which was attributable to *E. consputa* (Kluge and Siebert, 1985).

The Hakea seed-moth *Carposina autologa* Meyrick (Lepidoptera: Carposinidae), which attacks mature seeds in fruits escaping *E. consputa*, was expected to supplement adequately the weevil, and was introduced in 1970. Its biology and phenology have been described by Neser (1968); it is univoltine with no diapause, or quiescent phase, eggs being laid singly on the surface of mature fruits in the autumn. The eggs hatch a few weeks later and the larvae enter the fruit at a point along the suture on the adaxial surface of the fruit, only one larva developing per fruit. The larva initially feeds on one seed and attacks the other seed once the first has been consumed, both being needed to complete development. During the third instar, the larva prepares an exit tunnel through the woody fruit, alternating between feeding and excavating the tunnel. Mature larvae emerge from the completed tunnel, fall to the ground and pupate in the soil.

Field release was made by placing newly-hatched larvae onto fruits, inserting larvae directly on to fruits or releasing late instar larvae and moths; the most successful method being to insert larvae into holes drilled in the fruits (Dennill, 1987).

The insect was finally established at six sites in the southwestern Cape, four of which, however, were subsequently felled or burnt (Dennill, 1987; Dennill et al., 1987). The effect of *Carposina autologa* and *H. sericea* was evaluated at the two remaining sites (Paradyskloof and Stellenbosch Mountain) shortly after release. Infestation levels were low and population levels decreased over the study period (Dennill et al., 1987), partly from an indigenous fungal pathogen, *Colletotrichum gloeosporioides* (Penz.) Sacc., which caused the die-back and death of *H. sericea* (Morris, 1982; Dennill et al., 1987). This led to the suspension of the project in 1983.

However, during a visit to Paradyskloof to collect *H. sericea* seeds in 1987, it was discovered that many of the fruits contained emergence holes, indicating an increase in moth activity. It was therefore decided to re-evaluate *Carposina autologa* as a biological control agent. The aims of this study were, (1) to determine the level of infestation and population increase, (2) to assess the total seed destruction achieved by *Carposina autologa* on *H. sericea*, and (3) to examine the dispersal ability of the moth.

METHODS

Study sites

The study sites were situated at Paradyskloof (33°59'S 18°53'E) and Knorhoek (34°06'S 18°57'E), the two remaining release sites where *Carposina autologa* populations survived. Paradyskloof is situated on the south-facing slopes of the Stellenbosch Mountain and Knorhoek on the exposed north-facing slopes of the Hottentots Holland Mountains. The climate is mediterranean, humid-mesothermal (Csb) (Koppen, 1931), with an average rainfall of 1700 mm per annum, of which about 60% falls between May and August. The density of the *H. sericea* trees was 0.45 m⁻² and 1.8 m⁻² at Paradyskloof and Knorhoek, respectively. The height of the trees varied between 1 m and 6 m at Paradyskloof and 1 m and 3.5 m at Knorhoek.

At both sites, an area measuring 200 m × 100 m was marked out. Ten transects, 20 m apart, were laid across these plots. At 10 m intervals along each transect, the nearest healthy *H. sericea* tree was selected and permanently tagged. In this way, 91 and 100 trees were selected at Paradyskloof and Knorhoek, respectively. Only healthy trees were selected as many of the trees were infested with the fungus, *Colletotrichum gloeosporioides*.

Levels of infestation

Destructive sampling could not be used to determine the level of seed predation at the study sites because of low *Carposina autologa* population levels. The only clear way was to count the emergence holes. All the fruits on the sample trees were counted and examined for *Carposina autologa* emergence holes annually from 1988 to 1990. In spite of the height of some trees (5–6 m) and the abundance of fruits, which made the examination of the fruits difficult, the entire tree was sampled to circumvent the problems of sub-sampling. As each season's fruits are retained on the trees, all fruits with emergence holes were marked with a small dab of PVA paint to distinguish them in subsequent censuses. The paint used does not affect the behaviour of the moths. The annual increase in the number of attacked fruits was used as an indication of the population increase.

Counts were usually made during the summer and not immediately after larval emergence from the fruits because, (a) the larvae that pupate in the leaf litter or in the soil close to the surface would be trampled during sampling and (b) fruits are wet during winter, making it difficult to detect fruits with emergence holes. In the first year of study, the fruits sampled included newly-set fruits which would not have been available for egg laying. The reason for this was that the present study commenced late in the season and it was difficult to distinguish between old and new fruits. Fruits that had dehisced as a result of fungal damage were recorded separately because *Carposina autologa* do not oviposit on dehisced fruits (Neser, 1968).

Total seed destruction

Although counting emergence holes is a good measure of population increase, it is not an ideal measure of actual seed destruction, because, (a) larvae might die within the fruits after having destroyed one or both seeds and (b) seeds are also lost when fruit dehisce as a result of infection by the fungus, *Colletotrichum gloeosporioides*. Therefore, at the end of the study, all fruits were removed from the sample trees in September 1990 (3989 and 2155 fruits from Paradyskloof and Knorhoek, respectively) for examination under a binocular microscope to determine the fate of the seeds. As some of the fruits contained *Carposina autologa* larvae, this figure was used as an indication of the seed destruction for 1991 (see Table 1).

TABLE 1

Carposina autologa infestation levels on *Hakea sericea* at Paradyskloof and Knorhoek, 1988–1991

Site	Year	No. of fruits sampled	Mean % fruits attacked (\pm SE)
Paradyskloof ($n=91$)	1988	2583	36.7 (\pm 2.97)
	1989	2583	45.3 (\pm 3.13)
	1990	3070	51.7 (\pm 3.00)
	1991	3989	50.4' (\pm 2.83)
Knorhoek ($n=100$)	1988	1772	13.8 (\pm 1.94)
	1989	1772	29.9 (\pm 2.43)
	1990	1907	36.8 (\pm 2.56)
	1991	2155	40.7' (\pm 2.50)

'Includes fruits with larval *C. autologa*.

Dispersal

To obtain an indication of dispersal, *H. sericea* stands around some of the original release sites were selected for sampling. Because of the scarcity of

mature *H. sericea* infestations in the vicinity of the original release sites, only five suitable sites were sampled. At each site, 40 trees were randomly selected and felled. All the fruits on the trees were counted, noting the number with *Carposina autologa* emergence holes.

RESULTS AND DISCUSSION

Levels of infestation

The levels of infestation achieved by *Carposina autologa* at both Paradyskloof and Knorhoek were higher than initially expected. At Paradyskloof, the percentage of attacked fruits was 5.2% in 1982, increasing to 5.6% in 1983; whereas none of the fruits sampled contained fresh emergence holes in 1984 (Dennill et al., 1987). Four years later (1988), a mean of 36.7% of the fruits had emergence holes, which is a noticeable increase. Between 1988 and 1990, the mean number of fruits attacked increased to 51.7%. However, there was no further increase in 1991 (50.4%; Table 1).

At the Knorhoek site, the initial population comprised 574 larvae inserted into fruits, as described above, in 1981 (Kluge and Naser, 1991). From this release, 279 fully grown larvae successfully emerged from the fruits the following year. In 1988, 6 years later, 13.8% of the fruits sampled had emergence holes and by 1990 the mean number of attacked fruits had increased to 36.8% (Table 1).

The mean number of fruits attacked per tree increased steadily over the study period. Also, there was a corresponding decrease in the mean number of healthy fruits per tree between 1988 and 1990, despite the annual increment of new fruits. The 1991 level of infestation showed an increase in the mean number of fruits attacked at both sites, but no increase in the percentage of fruits attacked at Paradyskloof, as the mean number of healthy fruits increased markedly at this site (Table 1).

Total seed destruction

Based on the fruits returned to the laboratory in September 1990, 4.0% (± 1.29 SE) of the fruits showing no emergence holes had one seed consumed and 8.5% (± 1.78 SE) had both seeds consumed at Paradyskloof. At Knorhoek, the mean number of fruits without emergence holes, but with one or both seeds consumed was 5.4% (± 0.85 SE) and 8.4% (± 1.16 SE), respectively. Although this larval mortality appears to be high, this is cumulative and not annual mortality. If the number of destroyed fruits showing no emergence holes is added to the number of fruits with emergence holes, then the total mean seed destruction achieved by *Carposina autologa* at the end of

TABLE 2

Effect of the fungus *Colletotrichum gloeosporioides* on *Hakea sericea* fruits and trees at Paradyskloof and Knorhoek, 1988–1990

Site	Year	Total fruits	Mean % fruits diseased (\pm SE)	% trees diseased (\pm SE)	% trees dead (\pm SE)
Paradyskloof ($n=19$)	1988	2583	2.5 (\pm 0.51)	0	0
	1989	2583	7.0 (\pm 1.50)	30.8 (\pm 4.84)	2.2 (\pm 1.54)
	1990	3070	9.2 (\pm 1.38)	24.2 (\pm 4.49)	14.3 (\pm 3.67)
Knorhoek ($n=100$)	1988	1772	4.3 (\pm 0.96)	0	0
	1989	1772	7.9 (\pm 1.48)	32.0 (\pm 4.66)	1.0 (\pm 0.99)
	1990	1907	15.3 (\pm 2.40)	33.0 (\pm 4.70)	8.0 (\pm 2.71)

1990 at Paradyskloof and Knorhoek was 64.2% (\pm 3.00 SE) and 50.6% (\pm 2.97 SE), respectively.

At the start of the study, trees were selected that were free from fungus. After 3 years, 14% and 8% of the sample trees had died at Paradyskloof and Knorhoek, respectively. Some of the fruits on the remaining trees had dehisced as a result of *Colletotrichum gloeosporioides* attacks (Table 2). The seeds from dehisced fruits do not necessarily contribute to the *H. sericea* population as the seed is short-lived, and high seed loss if conditions are not favourable for germination. A significant proportion of seed is also consumed by granivores (Richardson and Manders, 1985).

The mean loss of fruit from the fungus increased during the present study from 2.5% and 4.3% to 9.2% and 15.3% at Paradyskloof and Knorhoek, respectively (Table 2). Dennill et al. (1987) found that after 2 years, 78% of the trees had died as a result of fungal damage. In 1990, the effect of the fungus on both *Carposina autologa* and *H. sericea* populations was not as devastating, total mean seed destruction by *Carposina autologa* and *Colletotrichum gloeosporioides* being 73.3% (\pm 2.98 SE) and 66.0% (\pm 2.70 SE) for Paradyskloof and Knorhoek, respectively.

Dispersal

The ability of the moth to disperse was most surprising. At Franschoek (19°09'S 33°56'E), 10.6% of the accumulated fruits were found to be attacked (Table 3). This colony originated from the Wemmershoek (19°10'S 33°52'E) site, 8 km away over the Wemmershoek Mountains. The Wemmershoek site was one of the first *Carposina autologa* release sites in the southwestern Cape, but was felled in 1983 when *Carposina autologa* population levels were still very low. The infestation levels at the other sites remained low, and it is probable that dispersal was wind-related.

TABLE 3

Carposina autologa effect on *Hakea sericea* at five sites near release sites

Site	No. of fruits	Mean % fruits with emergence holes (\pm SE)	Distance and direction from nearest release site
Franschhoek (19°09'S 33°56'E)	703	10.64 (\pm 2.52)	8 km South
Paarl (19°01'S 33°50'E)	5171	0.00	13 km West
Knorhoek dam (18°57'S 34°06'E)	2170	6.53 (\pm 1.79)	2 km North
Sir Lowry's Pass (18°57'S 34°08'E)	1587	0.00	2 km South-west
Jonkershoek (18°54'S 34°58'E)	26970	0.01 (\pm 0.03)	4 km North-east

CONCLUSIONS

Carposina autologa was introduced to reduce the large quantities of canopy-stored seed of *H. sericea*. At the end of 1990, *Carposina autologa* reduced the mean accumulated seeds at Paradyskloof and Knorhoek by 64.2% and 50.6%, respectively. Despite the fact that fruits are retained in the canopy and new fruits are being added annually, the annual increase in the rate of seed destruction by *Carposina autologa* was found to be greater than the rate of production of new fruits by the weed, except at Paradyskloof in 1991.

Whether this level of seed predation significantly reduces the recruitment of seedlings is not known. However, the seed reduction caused by *Carposina autologa* will limit the quantity of seed available for regeneration or recruitment after fires, and, in that sense, *Carposina autologa* has achieved the aims for which it was introduced. Pre-dispersal seed predation is only relevant if it reduces the seed density below levels at which the plant population will be reduced by density-dependent processes (Harper, 1977) and density-independent post-dispersal predation.

It is difficult to predict the level of predation needed to reduce the seed bank below the threshold level required to result in a decrease in the density of the plants. In the case of *Carduus nutans*, it was predicted that 99.9% of the seed would have to be destroyed by *Rhinocyllus conicus* to achieve control (Sagar, 1972), although a sustained reduction of the seed (around 50%) was enough to achieve control (Harris, 1986).

Predation of seeds is important to the dynamics of plant populations (Janzen, 1971; Harper, 1977). Seed loss reduces the distance at which a given density of seeds occurs from the seed source, i.e. the rate of dispersal. A reduction of 50% in the seed crop will halve the number of seeds reaching any

point in the dispersal range, and will alter the distance from the seed crop at which any particular density of seeds will land (Harper, 1977). A reduction in the number of seeds being dispersed will result in the formation of fewer nascent foci. Satellite foci can become the paramount problem for eventual weed control, even when the main infestation is allowed to grow unimpeded (Moody and Mack, 1988).

Richardson et al. (1987) suggest that the success of *H. sericea*, relative to other alien *Hakea* species, arises largely from the production of relatively large numbers of viable seeds. Because seed production is the only method of reproduction, control measures aimed at reducing the seed bank should provide the most effective means of combating *H. sericea*.

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