A review of established and new insect agents for the biological control of *Hakea sericea* Schrader (Proteaceae) in South Africa

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Hakea sericea **Schrader, an Australian proteaceous shrub or small tree, has become a major problem in nearly all the coastal mountain ranges and catchments of the southwestern and southern Western Cape Province. Biological control was initiated in 1970 and focussed largely on the release of insects that reduce seed production. Although the seed-feeding weevil *Erytenna consputa* Pascoe and seed-feeding moth *Carposina autologa* Meyrick became established, only *E. consputa* was considered to contribute to the reduction of the seed crop. The shoot-boring weevil *Cydmaea binotata* Lea, released in 1979 to suppress seedling regeneration, has mostly failed to establish and may only be surviving at one site. In this paper I review the biological control programme against *H. sericea,* focussing on the initiatives undertaken since 1990, which included (i) the redistribution of *C. autologa* and evaluations on its efficacy and (ii) host-specificity evaluations on the stem-boring beetle *Aphanasium australe* (Boisduval) and bud-feeding weevil *Dicomada rufa* Blackburn. *Erytenna consputa* continues to reduce the annual seed crop, especially in the southern Western Cape Province where natural and accidental fires are less frequent. *Carposina autologa* is considerably more effective than previously thought and populations are thriving at several sites where they were released in the 1990s. Host-specificity tests on *A. australe,* which also attacks *Hakea gibbosa* (Sm.) Cav., indicated that the beetle is suitable for release, and permission for its release in South Africa was sought in March 1999. Culturing difficulties with *D. rufa* precluded host-specificity tests in quarantine, but field evaluations in Australia strongly suggested that the weevil is host specific and an application for permission to release *D. rufa* will be submitted in 1999. The resumption of mechanical clearing operations in catchments invaded by *H. sericea* has necessitated the establishment of natural enemy 'reserves' to prevent the destruction, and possibly local extinction, of natural enemy populations.**

Key words: *Carposina autologa, Aphanasium australe, Dicomada rufa, Erytenna consputa,* biological control, *Hakea sericea.*

Hakea sericea Schrader (needlebush or silky hakea; Fig. 1) is an erect, single-stemmed, branchy shrub that grows to a height of 2–5 metres. It was introduced to South Africa from Australia during the 1930s as a hedge plant (Neser & Fugler 1978). However, the plant has become a major problem in nearly all of the coastal mountain ranges and catchments of the Western Cape Province (Fig. 2), where it often forms dense, impenetrable thickets and poses a serious threat to the floristically rich and unique mountain fynbos (macchia) vegetation. Isolated infestations occur in similar situations in the Eastern Cape Province.

The fruit of *H. sericea* is a woody follicle comprising two dehiscent valves, each valve containing one black, winged seed. The seeds, produced annually, are stored in the canopy and are only released after fires or when the plants die. Invasion has thus been intensified in the fynbos vegetation, where fires are a common and important feature and are necessary for species survival (Van Wilgen 1981; Van Wilgen & Richardson 1985). Factors that have contributed to the invasiveness of *H. sericea* in South Africa include its copious seed production and serotinous habit, high seed longevity in the canopy and efficient seed dispersal (Richardson *et al.* 1987). The biological control programme against *H. sericea,* which was initiated in 1970, has thus focussed on the use of seed-feeding agents to offset these features. In addition, the shoot-boring weevil *Cydmaea binotata* Lea (Curculionidae: Erirhininae) was released in 1979 to suppress seedling regeneration, but has mostly been ineffective at the few sites where it became established (Kluge & Neser 1991).

Kluge & Neser (1991) reviewed the biological control programme against *H. sericea,* including its taxonomy, introduction and spread in South

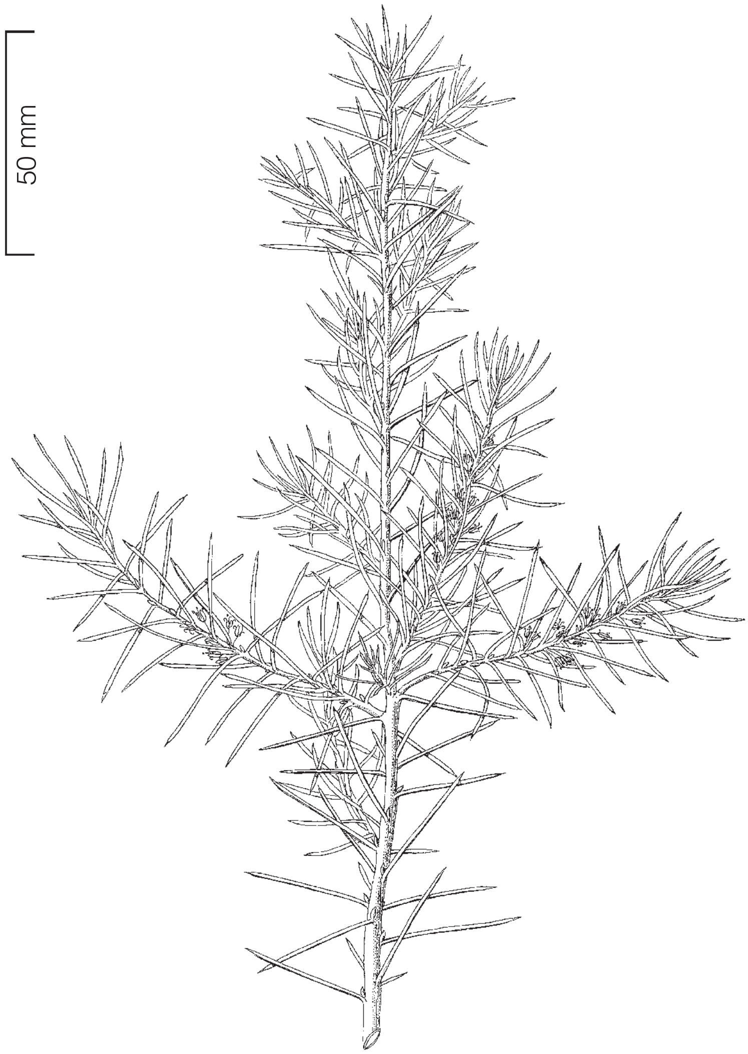

Fig. 1
Hakea sericea.
(Drawn by R. Weber, National Botanical Institute, Pretoria.)

Africa. By the late 1980s, the weevil *Erytenna consputa* Pascoe (Curculionidae: Erirhininae), which destroys the developing fruits of *H. sericea,* was the agent contributing most to the biocontrol programme. By contrast, the moth *Carposina autologa* Meyrick (Carposinidae), which attacks the mature seeds in fruits that had escaped *E. consputa* attack, was contributing little and comprised only three thriving field colonies. However, evaluations between 1988 and 1991 revealed that the moth was contributing more to biocontrol than previously thought. This review considers initiatives undertaken since 1990 and focusses on (i) the redistribution of *C. autologa* and evaluations on its efficacy, including factors that may have contributed to its slow establishment in South Africa, and (ii) prospects for releasing additional agents, following the renewed interest in the stem-boring beetle *Aphanasium australe* (Boisduval) (Cerambycidae) and the bud-feeding weevil, *Dicomada rufa* Blackburn (Curculionidae).

ERYTENNA CONSPUTA

In the previous review, Kluge & Neser (1991) concluded that *E. consputa* had not fully realized its potential and that the dramatic reduction in seed production recorded at Goudini in the southwestern region of the Western Cape had not been

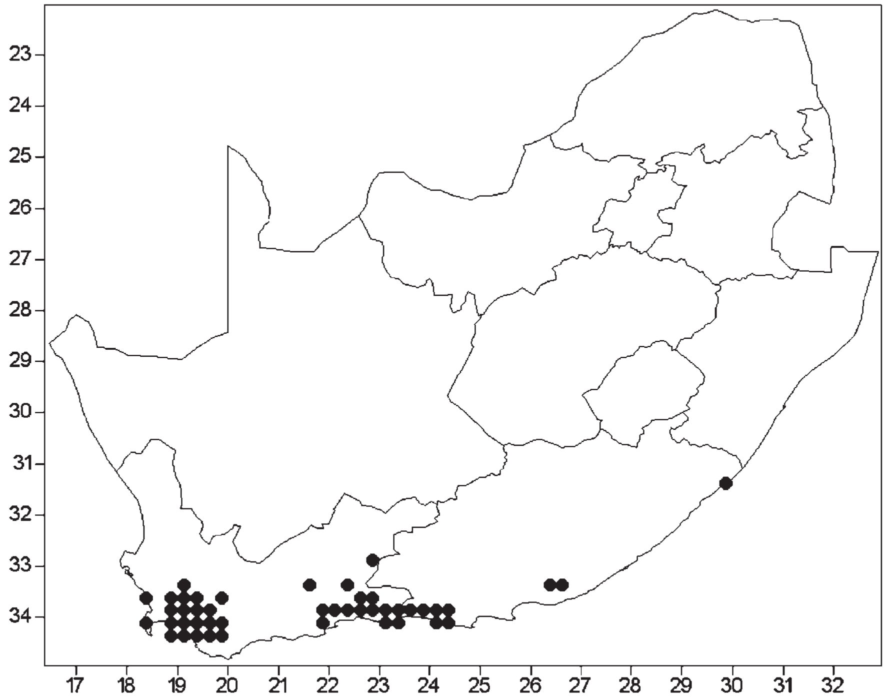

Fig. 2

Distribution of *Hakea sericea* in South Africa.

(Drawn by L. Henderson, Plant Protection Research Institute, Pretoria.)

consistently repeated elsewhere. Although the impact of the weevils has not been quantitatively monitored during the 1990s, recent field observations throughout the southern region of the Western Cape clearly showed that *E. consputa* populations have proliferated and are having a major impact on the annual seed crop. The absence of regular wildfires has accounted for the massive weevil populations in this region. Unfortunately, regular wildfires are restricting the weevils' effectiveness in the southwestern region of the Western Cape as the adults are slow to colonize plants that are regenerating after fires.

CYDMAEA BINOTATA

The current status of the shoot-boring *C. binotata* is unknown. Although Kluge & Neser (1991) recorded establishment at four of the 36 original release sites in the Western and Eastern Cape Provinces, it is likely that the weevils may only occur at one site now. Adults and larval feeding damage had regularly been observed at a site near Grahamstown (33.21S 26.37E) in the Eastern Cape (J.H. Hoffmann, pers. comm.), but this site has not been visited since 1990 and it is thus uncertain whether the population still persists. Indications are that *C. binotata* no longer occurs at the other three sites where establishment was reported. Earlier reports that, where established, the weevils were mostly ineffective in reducing the density of seedling populations (Kluge & Neser 1991), has meant that there have been no further attempts to reintroduce and establish *C. binotata.*

CARPOSINA AUTOLOGA

Neser (1968) described the biology and phenology of *C. autologa* (see Fig. 3). The moth is univoltine with no diapause or quiescent phase. In autumn, eggs are laid singly on the surface of mature fruits or between touching fruits. 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. Only one larva develops in each fruit. The larva initially feeds on one of the two seeds and only feeds on the second when the first has been consumed. Consumption of both seeds is necessary for the completion of larval development. The third instar larva prepares an exit tunnel through the woody fruit and alternates between feeding and excavating the tunnel. The mature (eighth instar) larva emerges from the tunnel, falls to the ground and pupates in the soil.

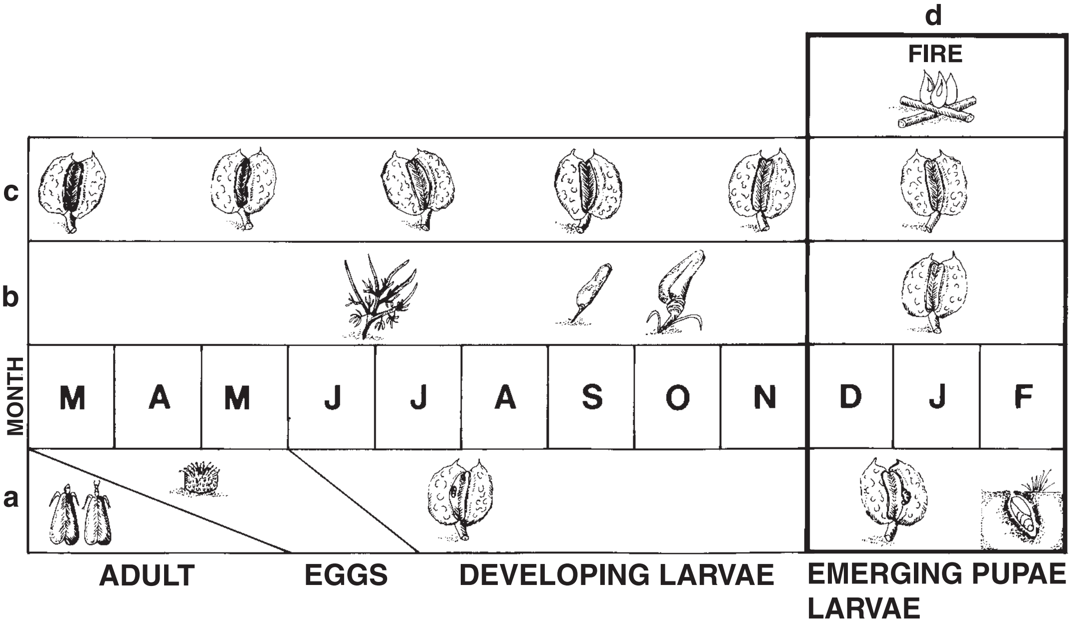

Fig. 3

The annual life cycle of *Carposina autologa* (a) in relation to the phenology of *Hakea sericea* (b). The presence of canopy-stored seeds (c) is indicated relative to the period of the year when wildfires are most prevalent (d) in the southwestern Western Cape Province.

(Drawn by L. Kilian.)

Redistribution and establishment of *C. autologa*

Carposina autologa was first introduced into South Africa in 1970 and some 18 788 eggs and larvae were imported between 1970 and 1982 (Kluge & Neser 1991). Initial attempts at establishing *C. autologa* in the field included releasing moths onto caged plants, placing neonates onto fruits in the field or inserting larvae directly into the fruits. Between 1978 and 1982, some 5150 larvae were released by inserting them directly into the fruit (Dennill *et al.* 1987). Although this method was refined to where up to 65 % of the larvae completed their development (Dennill 1987), it was both time-consuming and labour-intensive.

A new method was developed to redistribute *C. autologa* that involved attaching egg-bearing follicles to healthy fruits in the field. Fruits were harvested in the field during the egg-laying period, which mostly occurs during April and May in South Africa. The fruits were returned to the laboratory and inspected under an illuminating magnifier for confirmation of oviposition. The egg-bearing fruits were split in half, along the suture of the fruit, and the follicles with eggs were retained. The egg-bearing follicles were then attached to healthy fruits in the field, using a non-toxic adhesive.

Since 1990, some 11 546 egg-bearing follicles were released at 11 different sites in the Western Cape, using this technique (Table 1). Establishment has so far been confirmed at seven of these sites, with no establishment at one site. It is uncertain whether *C. autologa* has established at the remaining three sites. The moths have dispersed well and small, thriving colonies have been found up to 15 km from some of the release sites.

Impact of *C. autologa* on *H. sericea*

The impact of *C. autologa* on *H. sericea* was first evaluated between 1982 and 1984. Although *C. autologa* had become established at some sites, infestation levels were low and population levels decreased during the evaluation period (Dennill *et al.* 1987). This led to the suspension of the *C. autologa* programme in 1984. However, in 1987 collections of *H. sericea* seeds at one of the initial release sites revealed that many of the fruits contained larval 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.

Table 1

Releases of *Carposina autologa* at 11 sites in the Western Cape Province involving the attachment of egg-bearing follicles to healthy fruits of *Hakea sericea.*

Release site	Coordinates	Date	Number of follicles	Establishment
Burnsleigh (A)	33.51S 22.25E	June 1991	1081	Yes
Waboomskraal	33.51S 22.21E	June 1991	1403	No
Caledon	34.13S 19.25E	June 1991	767	Yes
Burnsleigh (B)	33.50S 22.26E	May 1992	759	Yes
Joubertina	33.49S 23.48E	May 1992	700	Uncertain
Steenboksberg	33.31S 19.07E	June 1992	635	Yes
		June 1995	500	Yes
		May 1996	758	Yes
Tsitsikamma Mts	33.56S 23.33E	May 1993	1000	Uncertain
Wellington	33.31S 19.02E	May 1993	1069	Yes
Ruitersbos	33.55S 22.01E	June 1994	729	Uncertain
Waaihoeksberg	33.33S 19.17E	June 1995	689	Yes
Villiersdorp	33.58S 19.16E	June 1997	1456	Yes

Studies at Paradyskloof (33.58S 18.53E) and Knorhoek (34.06S 18.57E) in the southwestern region of the Western Cape, between 1988 and 1991, showed that by the end of 1990, *C. autologa* had reduced the mean numbers of accumulated seeds by 64.2 % and 50.6 %, respectively (Gordon 1993a). Despite the retention of fruit in the canopy and the annual addition of new fruit, the annual increase in the rate of seed destruction by *C. autologa* was found to be greater than the annual rate of production of new fruit by the weed, except at Paradyskloof in 1991. Recent field observations revealed that *C. autologa* had destroyed an estimated 80 % of the accumulated seeds at some sites (C. Burgers, pers. comm.).

Factors influencing the efficacy of *C. autologa*

Despite these promising results, several factors were observed to reduce the effectiveness of *C. autologa* in South Africa. One of these is the death and die-back of trees that are infected by an indigenous fungus, *Colletotrichum gloeosporioides* (Penz.) Sacc. The fungus was first noted in the southwestern Cape in 1964 (Taylor 1969) and typical symptoms of the disease are stem and branch lesions that exude large quantities of colourless gum, which later turn reddish brown (Morris 1982). When these lesions girdle the stem or branches, it effectively ring-barks the plant, causing die-back. The plant invariably dies when girdling takes place lower down on the main stem or at ground level. When *H. sericea* trees and branches die as a result of the fungus, the accumulated fruit on the affected trees or branches dehisce and the seeds fall to the ground. In areas where climatic conditions favour disease development, high levels of mortality may occur (Morris 1991).

This fungal-induced seed loss occurs at a crucial stage during the development of *C. autologa.* Most of the infected plants die and release their seeds between October and January (Richardson & Manders 1985). This overlaps with the time at which larval emergence for pupation reaches a peak (December and January) and is disruptive if the majority of larvae are not ready to pupate. Immature larvae will thus die as the chances of them finding and entering new fruit is remote. At low *C. autologa* population levels, a high incidence of fungal attack can have a devastating effect on moth emergence and subsequent larval densities. Ideally, *C. autologa* release sites should be selected in areas where the fungus is absent or occurs at low levels.

Another factor that constrains *C. autologa* populations is the apparent inability of the moths to distinguish between healthy and previously-attacked fruits for oviposition. Evaluations at Paradyskloof in 1990 revealed that some 42.5 % of the eggs were deposited on previously-attacked fruits from the previous season (Gordon 1993b). The moths' preference for fruits of a particular architecture, notably 'knobbly' fruit, has caused these repeated ovipositions on the same fruit, year after year. This results in excessive larval mortality because few neonate larvae will be able to locate and enter pristine fruit. Mortality of these exposed larvae will also be aggravated by predation and unfavourable weather conditions.

The relative timing of wildfires, both natural and accidental, in the Western Cape is further diminishing the impact of *C. autologa.* The seeds of *H. sericea* are borne in heat-resistant follicles and are released *en masse* after fires, resulting in considerable seedling recruitment. Periodic wildfires are a feature of the fire-adapted, mountain fynbos vegetation invaded by *H. sericea* (Bond 1980) and are generally concentrated in the summer months of December to February (Van Wilgen 1981). At this time the fruit of the latest seed crop mature but, since oviposition by *C. autologa* occurs much later (March to May), the fire-dehisced seeds escape attack by *C. autologa* (Fig. 3). Consequently, even if *C. autologa* destroys all of the previous season's accumulated fruit, the latest season's unattacked fruit will always be available to initiate seedling recruitment during this critical wildfire period.

APHANASIUM AUSTRALE

Webb (1964) considered the stem-boring weevil *A. australe* to be a prime candidate agent for *H. sericea,* but both Moore (1964) and Neser (1968) expressed reservations about its effectiveness as many of the plants survived larval attack. However, there was renewed interest in *A. australe* in 1982, and later in the mid 1990s, largely because it also attacks the related weed *Hakea gibbosa* (Sm.) Cav. (rock hakea), which is not attacked by the existing biocontrol agents or by the native fungal pathogen, *C. gloeosporioides.* Although *A. australe* does not normally kill plants growing under natural conditions, it is envisaged that trees subjected to stress (e.g. from drought or disease) may be killed by larval damage. The extensive tunnelling may weaken the plants structurally and cause them to topple over, and larval damage may also assist fungal infection.

Biology and host specificity of *A. australe*

The adults of *A. australe* are blackish brown and about 20 mm in length. Clusters of 10–20 eggs are deposited on the base of the stem (Neser 1968). The neonate larvae enter the stems directly from the eggs and reddish brown mucilage is exuded by the plant tissue at the larval entry points. The larvae of *A. australe* tunnel gregariously at the base of stems and in the sub-surface roots of the plants. The bases of the stems have a characteristic thickening due to the formation of scar tissue. The larvae avoid the tunnels of conspecifics by diverting their course when approaching another tunnel. The larvae develop slowly and may take one to two years to reach maturity. Pupation occurs in hollow chambers, beneath the bark and just above the soil surface, which are excavated by the mature larvae.

Initial host-specificity testing started in 1982, following the first introductions of *A. australe* from Australia. During choice tests involving 12 Australian and six South African species of Proteaceae, oviposition was only recorded on Australian species of *Hakea* and *Grevillea,* both in the tribe *Grevilleae* (Kluge, unpubl.). However, further work on *A. australe,* which has a two-year life cycle, was suspended in 1983 because of difficulties associated with culturing and host-specificity testing, and doubts about obtaining sufficient numbers of insects from Australia to allow successful establishment.

Although the mechanical control programme against hakea was initially successful (Fenn 1980) this later encountered financial problems (Kluge & Neser 1991) and *A. australe* was reconsidered as a potential biocontrol agent. Stems and roots containing larvae were collected in Australia during July in 1995 and 1996 and introduced into quarantine. The adults emerged approximately six months later and were allowed to mate so that eggs could be collected for subsequent testing. No attempt was made to rear larvae on a synthetic diet, as this had achieved limited success in the past.

Host-specificity tests were resumed in 1996 and comprised no-choice tests in which three *A. australe* eggs were attached to the stem-bases of potted plants of *H. sericea* and several test species. Of the 66 test plant species from 15 families, larvae of *A. australe* only developed on one introduced species of *Grevillea,* confirming the results of the earlier choice tests. By contrast, all of the larvae entered and developed in the stems of *H. sericea* and *H. gibbosa.* These trials indicated that *A. australe* is suitable for release, and permission for its release in South Africa was sought in March 1999.

This recent progress contrasts with previous attempts to rear and test *A. australe* in the early 1980s, when much time was wasted in trying to rear *A. australe* on a synthetic diet. The present system of importing infested *H. sericea* stems, and

Table 2

A chronological record of the number of *Dicomada rufa* adults imported into South Africa from Australia.

Date	Origin	Collector	Number consigned
May 1976	Wilson's Promentary, Victoria	P. van der Duys	348
Sept. 1993	Bargo, New South Wales	S. Neser	440
Sept. 1994	Bargo, New South Wales	S. Neser and A.J. Gordon	800
June 1995	Bargo, New South Wales	A.J. Gordon	800
June 1997	Bargo, New South Wales	A.J. Gordon	1412

allowing the adults to emerge naturally in quarantine, is far more efficient and insect emergence is better synchronized. The method of attaching eggs to the stems of potted plants has also resulted in a strong laboratory culture, in excess of 1000 larvae, and can be used to mass-rear *A. australe* once permission for release has been obtained.

DICOMADA RUFA

There is very little biological information on the bud-feeding weevil *D. rufa.* The adults are dull-brown, 2–3 mm in length and feed predominantly on the dormant axiliary buds. The eggs are laid singly in the reproductive buds of the plant. The larvae feed on the inflorescences and young succulent vegetative growth, in capsules formed by the cementing together of individual flowers or young leaves. Despite the lack of biological information, the weevil has a high priority because of its ability to limit fruit set in the field.

Host specificity of *D. rufa*

Adults have been collected on *H. sericea* at sites around two localities in Australia and introduced for culturing and host-specificity testing (Table 2). Following the first introduction in 1976, preliminary host-specificity tests were conducted. During these trials, adults fed on the inflorescences of *Hakea* and *Grevillea* species but not on any of the test species from the seven genera of South African Proteaceae that were presented (Gunn, unpubl.). These tests were later suspended because of culturing difficulties and, despite further importations of weevils between 1993 and 1995, testing was only resumed in 1997. However, during larval no-choice tests conducted in 1997, the larvae failed to survive on *H. sericea* and the tests were deemed inconclusive. Attempts at culturing *D. rufa* in quarantine were similarly characterized by poor larval survival. Although some oviposition occurred, few larvae reached maturity and no adults were ever recovered.

Because of the problems of culturing *D. rufa* in quarantine, data on its host specificity was obtained by means of field surveys of the indigenous vegetation that was related to (and in close proximity to) *H. sericea* growing naturally in Australia. These surveys were based on the approach of Balciunas *et al.* (1996) and were undertaken during June in 1997 and 1998. Some 45 plant species, growing in the vicinity of *H. sericea* that were infested with *D. rufa,* were examined for signs of *D. rufa* adults and/or feeding damage. There was no evidence of feeding on any plants other than *H. sericea.* Two adults of *D. rufa* were found on a single plant of *Acacia terminalis* (Salisb.) MacB. (Fabaceae), but these appeared to be only resting on the plant as there were no signs of feeding. Indeed, further searches on 10 additional plants of *A. terminalis* yielded only one adult. These field observations strongly suggested that *D. rufa* is host specific and thereby suitable for release in South Africa. Based on these results, permission for the release of *D. rufa* in South Africa will be sought in 1999.

INTEGRATED CONTROL

The recently inaugurated 'Working for Water' Programme, which is aimed at the mechanical clearing of alien invasive plants from rivers and water catchments countrywide, has targeted *H. sericea* in the catchments of the Western Cape. Mechanical control is an extremely effective method of controlling *H. sericea* (Fenn 1980), but biological control needs to be in place to prevent resurgences of the weed and limit follow-up operations. However, mechanical clearing can be antagonistic to biocontrol and could cause local extinctions of agents if *H. sericea* populations are temporarily removed. Seed-feeding species are particularly at risk because *H. sericea* seedlings will recolonize cleared areas and these will not be able to support insect populations until the plants start to set fruits after several years.

One solution would be to utilize agents that disperse rapidly and have good host-locating abilities, as this would allow them to recolonize resurging populations of *H. sericea.* Unfortunately, both seed-feeding agents currently established on *H. sericea* (*E. consputa* and *C. autologa*) are slow to recolonize burnt or cleared areas and it is suspected that the same holds for *A. australe.* By contrast, the bud-feeding weevil *D. rufa* is a rapid disperser and would thus be better suited to an integrated control programme. *Dicomada rufa* should thus retain its high priority, despite the difficulties associated with culturing and later mass-rearing.

The establishment of natural enemy 'reserves' or refuges is another strategy to prevent established agents from being eliminated by clearing operations (Kluge 1983). In addition, these will serve as foci from which recolonization of resurging *H. sericea* populations can occur and collections of agents for redistribution can be made. Ideally, 'hakea reserves' should be around 1–5 ha in size and 5–10 km apart and should consist of plants in their reproductive phase. The fungus should be excluded and the plants should be situated upwind so that the prevailing winds will facilitate the dispersal of the agents. The reserves should also be situated in areas suitable for optimal insect development and should be protected from wildfires by firebreaks.

CONCLUSIONS

Seed-feeding insects continue to contribute to the biological control of *H. sericea* in South Africa, although their impact is constrained by several factors, notably fires. Despite earlier pessimism about the effectiveness of *C. autologa,* recent evaluative studies have demonstrated that, despite several constraints, the moth has proliferated and is destroying significant amounts of *H. sericea* seeds. The new method of attaching egg-bearing follicles to healthy fruits in the field has proved to be extremely quick and effective and additional releases of *C. autologa* should thus be made throughout the weed's distribution in South Africa. Recent progress in evaluating the host specificity of the stem-boring *A. australe* and bud-feeding *D. rufa* has ensured that releases of both agents may be imminent. The integration of established biocontrol agents with the clearing campaign of the 'Working for Water' Programme presents a future challenge. The use of agents with specific qualities (*e.g.* good dispersal) and the creation of natural enemy 'reserves' are essential for successful integrated control of *H. sericea.*

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