# The Potential Role of *Bruchophagus acaciae* (Cameron) (Hymenoptera: Eurytomidae) in the Integrated Control of *Acacia* Species in South Africa

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#### Abstract

Australian acacias invade watersheds and riverbeds in South Africa, reducing water flows and threatening environmental and economic values. Acacia mearnsii is the most widespread and important weed but also forms the basis of an important industry. A. dealbata, and to a lesser extent A. decurrens are also problems. All belong to the Section Botrycephalae of the sub-genus *Heterophyllum*. Short term control is achieved locally by removing plants, and by using herbicides, but seed-feeding control agents may provide an acceptable solution in the long term. Larvae of Bruchophagus acaciae (Cameron) (Hymenoptera: Eurytomidae) develop in the seeds of acacias. It was described from New Zealand, but is an Australian species. We explore whether B. acaciae has a role as a control agent for acacias in South Africa. Seed was collected from 28 Australian species of Acacia growing in New Zealand. Attack was restricted to four of the seven species within the Section Botrycephalae, and two cases of attack on Acacia rubida (Section Phyllodineae; n=9). Apart from a wasp reared from one seed, A. mearnsii was not attacked, possibly because suitable pods were not available during the oviposition period of the wasp. Seed destruction in A. dealbata and A. baileyana averaged 47% (range 4 to 96%). Potential fecundity averaged 91 eggs per female. Field emergence and oviposition in spring coincided with the presence of fully-formed green seeds within developing pods, but the oviposition period was only 20-30 days long. Wasps overwintered as larvae within seeds, and survived well over the wide range of storage methods and conditions tested. B. acaciae appears restricted to acacias within one section of the sub-genus Heterophyllum, and probably poses no threat to African species which belong to the subgenus Acacia. It appears capable of reducing the seed production of several species significantly, but lack of damage to A. mearnsii seeds may limit its value as a control agent.

Keywords: Biological control, acacia, seed, New Zealand, South Africa

#### Introduction

A number of Australian *Acacia* species were introduced into South Africa in the early nineteenth century as ornamentals, for timber, and to stabilize drifting sand. Many of these have become invasive, and now threaten conservation areas, dune ecosystems, and the potential of agricultural land (Dennill and Donnelly 1991). Larger *Acacia* species also severely affect scarce water resources by obstructing watercourses, and reducing water

flow by transpiration. The species that are most responsible for this are *Acacia mearnsi* De Wild, *A. dealbata* (Link), and *A. decurrens* (J.C. Wendl.). Although *A. mearnsii* is an invasive weed, it is also valued as a source of tannin, timber, firewood, and other products (Dennill and Donnelly 1991).

The South African government has responded to the threat posed by invasive species by developing the *Working for Water* program. This is a collaborative program that aims not only to ameliorate the problems caused by *Acacia* species and other invasive plants in the short term, but also to provide sustainable solutions in the long term. Watercourses and catchments are cleared of invading weeds by workers using mechanical and chemical control methods. The program has more than 30 projects in eight provinces, and employs thousands of workers, more than 50% of whom are women. In this way, the program furthers the government's commitment to reconstruction and development by creating jobs, business opportunities, and by empowering local communities to care for water and their natural environment. The program acknowledges that this type of control must be reapplied indefinitely, and is too expensive to provide a long term solution. The need for sustainable control methods for invasive acacias is acknowledged, and the development of biological control options is an integral part of these management strategies (ARC/LNR 1997, Zimmerman and Neser 1999).

Biological control projects have been initiated against eight Australian acacia species, and the closely related *Paraserianthes lophantha* (Willd.) Nielson (=*Albizia lophantha*) in South Africa. *Trichilogaster acaciaelongifoliae* Froggatt (Hymenoptera: Pteromalidae) and *Melanterius ventralis* Lea (Coleoptera: Curculionidae) have been introduced against *Acacia longifolia* (Andr.) Willd., *Trichilogaster* sp. against *Acacia pycnantha* Benth., *Melanterius acaciae* Lea against *Acacia melanoxylon* R.Br., *Melanterius servulus* Pascoe against *P. lophantha* and *Acacia cyclops* A. Cunn.ex G. Don., *Melanterius maculatus* against *Acacia mearnsii*, *Melanterius* sp. against *Acacia dealbata* and *Acacia decurrens* (Dennill and Donnelly 1991), and a rust fungus, *Uromycladium tepperianum* (Sacc.) McAlp. against *Acacia saligna* (Labill.) Wendl. (Morris 1991).

Bruchophagus acaciae (Cameron) (Hymenoptera: Eurytomidae) is a wasp that develops in the seeds of some Acacia species. It was first described in 1910 from specimens reared from acacia seeds in Canterbury, New Zealand (Cameron 1910). However, it clearly originated in Australia, as New Zealand has no native acacias. Cameron named the host as black wattle, or "A. decurrens". In fact, black wattle is the accepted common name for A. mearnsii, and so the original host remains obscure. B. acaciae is represented in only two of the major collections in New Zealand. It has been collected from 7 sites, all in the South Island. B. acaciae is univoltine, and larvae overwinter inside fallen seeds. Adults emerge in November, just as many acacia pods reach full size. As seeds mature, larvae create two characteristic, frass-filled holes in the distal end of the seed. This frass cements infested seed to the pod valve, and cements the valves together at each infested seed. Kluge (1989) observed this in some Bruchophagus-infested seeds in Australia. Infested seed is not ejected from such pods at dehiscence, and twisted pods that fall from the tree often blow in the wind before lodging far from the parent tree. Larval development is completed before seed-fall in December and January.

Insects were observed emerging from the seed of *Acacia dealbata*, *A. baileyana* F. Muell., and *Acacia irrorata* Spreng. in the Canterbury region in 1984. Infestation rates were described as high (Dr. J. Sheppard, personal communication). Insects were also recorded emerging from *A. rubida* A.Cunn. seeds. The insects were not formally identi-

fied, but were probably *B. acaciae*. With the possible exception of *A. rubida, B. acaciae* was only recorded from bipinnate wattles (Section Botrycephalae) prior to this study. *B. acaciae* is one of five phytophagous eurytomids recorded in New Zealand (Valentine 1970, Valentine and Walker 1991). All are exotic, but are attacked by a range of generalist parasitoids, including a *Tetrastichus* sp. Despite this, there are no records of parasitism of *B. acaciae* in New Zealand (Valentine 1967).

Approximately 150 Australian species of *Acacia* have been reported as either naturalized or in cultivation in New Zealand (E. Nicol, Landcare Research database, personal communication) although the status of many of those records is questionable. The taxonomic status of the genus *Acacia* (sensu lato) has been the subject of at least three taxonomic treatments in the last 30 years. For this study, the nomenclature provided by Pedley (1978) has been used. All of the *Acacia* species that were monitored belong to the subgenus *Heterophyllum*, which is further divided into five sections.

Field observations and the few available literature records in New Zealand suggest that the host-range of *Bruchophagus acaciae* may be restricted to *Acacia* species of Australian origin. The aim of this research was to determine whether this species might be an appropriate biological control agent for some of the Australian acacias that have become weeds in South Africa. This paper examines the field host-range of *B. acaciae* in New Zealand, its fecundity, and certain life history characteristics such as oviposition and emergence phenology.

#### Materials and Methods

# Field Host-range of Bruchophagus acaciae

Trees were sampled at 24 sites, 7 in the North Island, and 17 in the South Island. Most samples were taken from four *Acacia* plantations in Canterbury, originally established to test the efficacy of a range of these species for stabilizing soil erosion (J. Sheppard, personal communication). Development of pods on bipinnate acacias during spring was monitored almost daily. Seeds were harvested from the trees when pods were almost dry, but before significant pod dehiscence had occurred. The dates on which the pods of each species matured differed little from year to year, or from site to site, but the timing of seed-fall varied greatly between species. The bipinnate acacias shed seed over a 2-week period from about December 20 in 1997, and December 26 in 1998. Samples were taken between December 20 and February 15 in 1997/98 and 1998/99. Pods were sampled by taking at least five bunches of at least 30 pods haphazardly from around the tree, at 0-2 m above the ground. Pods were stored in paper bags at room temperature. Seeds were stripped by hand from the pods, and stored in paper envelopes. Over the following months, seeds were counted and examined, and infestation rates were calculated.

#### Emergence Phenology

In September 1998, four pod samples were collected from the ground around an *A. dealbata* tree at Lincoln, Canterbury. Samples one and two contained pods that had lodged in the shade against a building. Sample three was taken near an air-conditioning unit generating warm air. The fourth sample was taken in full sun beneath the tree. Pods from each area probably experienced different exposure to weather conditions after falling from the tree during the previous summer, although these conditions were not recorded. Pods were stored in closed plastic boxes that were then placed under a building to complete development in the same ambient air temperatures. Boxes were examined at regular intervals in spring, and the number of wasps emerging was recorded.

# **Oviposition Period**

On 4 November 1998, 30 shoots on two *A. dealbata* trees at Lincoln, Canterbury, were haphazardly selected, and all but five were enclosed in cloth bags. These five were left for one week, to expose pods to *B. acaciae* oviposition. After one week, exposed pods were bagged, and a further five randomly selected bags were opened. This was then repeated at 10-day intervals. Each bag enclosed at least 30 developing pods. Five bags remained enclosed throughout the experiment to measure oviposition activity prior to the experiment. In late December, pods from these shoots were harvested, seeds were extracted, and the level of infestation was determined. Data for all shoots within an exposure period were pooled. The experiment was repeated on one *A. dealbata* tree at Landale, Canterbury, but shoots were bagged 6 days later than at Lincoln. Only two shoots were exposed at each site from 9-21 December. The number of seeds examined in other periods varied from 642 to 1,242 per bagged shoot.

# **Potential Fecundity**

Twenty newly-emerged female *B. acaciae* were dissected, and the eggs present in the ovarioles were counted.

#### Results

# Field host-range of Bruchophagus acaciae

Seeds of 29 plant species were collected, 184 pod samples were taken over two seasons, and a total of 49,845 seeds were examined. Of the 29 species sampled, 23 were not attacked in either season (Table 1). *P.lophantha* was not attacked. In contrast, *A. baileyana*, *A. dealbata*, *A. decurrens*, *and A. silvestris* Tindale were consistently attacked in both years. Of 76 pod samples taken from these species in the South Island, only one was not infested.

The four affected species belong to the Section Botrycephalae (Pedley 1978). *A. mearnsii* also belongs to this Section of the sub-genus, but only one infested seed was found among the 5,513 seeds collected at 13 sites over the two years. Seed samples of other members of the Section were not infested (Table 1).

Seeds contained in two samples taken from *A. rubida* at Orana Park, Canterbury, in 1997/98 were not infested. However, in 1998/99, two samples each yielded one infested seed (0.6% infestation). *B. acaciae* was not present in the four other samples taken at three sites that year, but informal collecting at Orana Park revealed that it was present in pods on all five trees sampled.

The proportion of the annual seed crop attacked by *B. acaciae* varied between hosts, between sites, and between years. *A. baileyana*, *A. dealbata*, and *A. silvestris* appear to be better hosts for *B. acaciae* than *A. decurrens*. (Table 1). Wasps attacked over 90% of *A. dealbata* seeds at some sites, but infestation at Junville averaged less than 10% in both years. Far more seeds were affected in 1997/98 than in 1998/99. The distribution of infestation rates between sites is illustrated in Fig. 1. *B. acaciae* was not recovered from any seeds collected in the North Island. It is possible that this species is not present there.

# **Emergence Phenology**

Sixty-seven percent of all wasps that emerged did so over a short period of 6 days, beginning on 6 November 1998 (Fig. 2). The emergence pattern varied. In samples one and two, 81% and 72% of wasps emerged during this period. Three percent of wasps

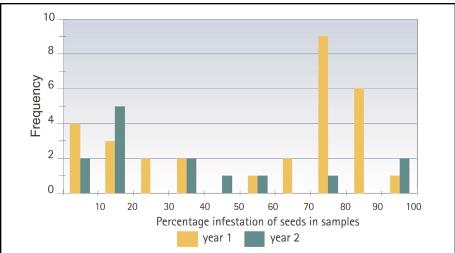
Table 1. Infestation by Bruchophagus acaciae of seed of 28 species of Acacia collected at many New Zealand sites in 1997/98 and 1998/99.

Subgenus Section	Species	1997/98 sites	samples	seeds	Mean % infested	1998/99 sites	samples	seeds	Mean % infested
ACACIA	baileyana	4	7	1,645	62.2	6	10	3,545	20.6
Heterophyllum	•								
Botrycephalae									
	cardiophylla	0	-	-	-	1	1	37	0
	dealbata	9	16	12,566	58.3	6	12	2,335	46.9
	deanei	1	3	201	0	1	2	177	0
	decurrens	5	8	1,340	27.0	3	3	219	9.9
	mearnsii	8	16	3,361	< 0.1	6	11	2,152	< 0.1
	pruinosa	0	-	-	-	1	1	10	O <sup>a</sup>
	silvestris	2	6	1,684	78.7	2	4	780	63.4
Phyllodineae	boormanii	1	4	1,428	0	1	1	115	0
	brachybotria	0	-	-	-	1	1	386	0
	falciformis	1	4	361	0	1	1	0	-
	genistifolia	1	2	633	0	1	1	48	0

<sup>&</sup>lt;sup>a</sup> Indicates 0% infestation in controls

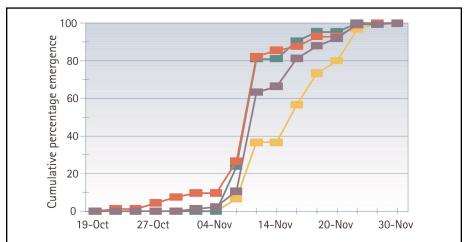
Section	Species	1997/98 sites	samples	seeds	Mean % infested	1998/99 sites	samples	seeds	Mean % infested
	leprosa	0	_		_	1	1	260	0
	myrtifolia	0	_	-	_	1	1	380	0
	penninervis	1	3	303	0	_	_	-	-
	pravissima	2	6	3,026	0	1	3	1,545	0
	retinodes	3	4	1,457	0	1	1	425	0
	rubida	1	2	382	0	3	7	1,658	< 0.1
	verniciflua	1	3	1,566	0	3	3	472	0
Juliflorae	alpina	0	-	-	_	1	1	93	0
	doratoxylon	0	-	-	_	1	1	23	0
	floribunda	0	-	-	-	1	1	220	Oa
	longifolia	0	-	-	_	1	3	477	0
	mucronata	1	3	481	0	1	0	0	-
	verticillata	0	-	-	-	1	2	91	0
Plurinervia	melanoxylon	1	0	0	0	3	1	240	0
	riceana?	0	-	-	-	1	1	70	0
Pulchellae	pulchella	1	1	255	0	1	2	425	0

<sup>&</sup>lt;sup>a</sup>Indicates 0% infestation in controls



**Fig. 1.** The frequency of the percentage of *A. dealbata* seed infested by *B. acaciae* at all sites. The list of sites sampled was similar but not identical between years.

emerged before this date, all in samples three and four, the samples thought to have experienced warmer conditions in early spring than samples one and two. Although emergence peaked in the second week of November, some wasps continued to emerge until November 23. Only 1% of wasps emerged after this date. The median emergence dates in the four samples were 9, 9, 11, and 15 November.



**Fig. 2.** The pattern of emergence of *B. acaciae* adults. Symbols indicate results from four discrete samples of seed collected from the ground within a 20 m radius in spring, and emerged in outdoor conditions.

# **Oviposition Period**

At Landale, 55.1% of all seeds exposed to *B. acaciae* in this experiment were affected. Oviposition activity peaked in the period 10-20 November, when 69% of the affected seed was attacked, and by November 30, 95.3% of all recorded oviposition was completed.

At Lincoln, peak oviposition appeared to occur slightly earlier than at Landale. Only 20.7% of all seeds exposed were infested, but of those, eggs were laid in 56.6% from 4-11 November, and in 78.4% from 4-20 November. A small proportion of the seeds that were naturally exposed before the experiment began was infested. This indicates that some wasps emerged in the field earlier than was indicated by the emergence time experiment. One of the five shoots exposed for the first time from 9-21 December was also infested. However, this infestation may also have occurred before 4 November.

The natural level of seed infestation in experimental trees at Landale was 48.1% (SEM=3.9, n=10), and at Lincoln it was 14.3% (SEM = 6.7, n=5). These figures were similar to the sum of infestation rates across the observed oviposition periods (55.7 and 20.7% respectively).

# **Potential Fecundity**

The potential fecundity revealed by dissection was 91±5 eggs per female (n=20; range 57 to 146). There was some evidence that this species is synovigenic, which means that lifetime fecundity may be slightly higher than that recorded by dissection.

#### Discussion

This is an unusual study. Normally, novel research of this type would occur in the home range of the agent, where the agent is relatively unknown, relatively rare, and subject to population pressure from parasitoids, predators and diseases. Naturalization of *B. acaciae* in New Zealand has allowed its value as a control agent to be assessed for the first time, not only in the absence of its natural enemies, but also in population densities that resemble those likely to develop if the species is released in South Africa. This adds weight to some of the conclusions that can be drawn.

There is strong evidence that *B. acaciae* has a narrow host range. A large number of *Acacia* seeds collected from 29 species of Australian *Acacia* species were examined. *Bruchophagus acaciae* was recorded from only five of them. These all belong to the bipinnate acacias: the section Botrycephalae of the sub-genus Heterophyllum. There was one exception to this. Wasps emerged consistently, but at very low levels from seeds of *A. rubida* collected at Orana Park. This species belongs to the 'Racemosae group' of the section Phyllodineae. This group is considered to be closely-related to the Botrycephalae. Several species retain features intermediate between these groups, and *A. rubida* sometimes bears bipinnate and phyllodinous foliage on the same shoot. Pedley (1986) suggests that the Botrycephalae may have arisen from the 'Racemosae group'.

As no other seed-feeding insects were encountered in Canterbury during this study, the insects recorded emerging from seeds of *A. irrorata* collected in Canterbury (J. Sheppard, personal communication) were probably *B. acaciae*. However, *B. acaciae* did not affect seeds of all species within the Botrycephalae. Only two of over 5,000 *A. mearn-sii* seeds examined were infested. *A. deanei* seeds also appeared to escape damage. Too few seeds of *A. cardiophylla* were examined to say with certainty that this species was immune. *A. pruinosa* seeds collected in the North Island were not attacked by the wasp,

but no B. acaciae were reared from susceptible controls either.

This study was limited geographically, but the results strongly suggest that *B. acaciae* is functionally specific to certain *Acacia* (*Heterophyllum*) species within the Section Botrycephalae. The host-specificity acts below the sub-generic level. This suggests that African acacias, which belong to the sub-genus *Acacia* of the genus *Acacia*, are unlikely to be affected. Pedley (1986) has proposed that a new genus (*Racosperma*) should be erected for the Australian acacias. If this concept becomes more widely accepted, Australian and African species will belong to separate genera, reinforcing the taxonomic distance between susceptible hosts and African acacias.

There are two possible explanations for the host-specificity of *B. acaciae*. Specificity may be mediated by phytochemical or biophysical differences between species, as it is for many host-specific insects. However, differences in the flowering phenology of potential may also be important. *B. acaciae* adults were active for only a short period of the year. Adults emerged over a short 6-day period. Oviposition probably began in early November at Lincoln (and a little later at Landale), and was completed 4 weeks later. Most oviposition occurred over a single 10 day period. Sampling periods were 10 days long, and it is possible that the effective oviposition period is as short as 3 weeks. *A. mearnsii* and *A. deanei* are not hosts. These species differ from most bipinnate species in flowering in late summer and autumn, and carrying protopods through winter. Pods begin to develop earlier in spring than those of susceptible hosts, and may be unsuitable for oviposition by the time *B. acaciae* begins to emerge in early November. However, while flowering phenology may be an important factor in defining host-range, it is not the only one. Most phyllodinous species flowered and produced pods at the same time as susceptible bipinnate species, and yet were not affected.

This has important implications for the timing of any oviposition tests in South Africa, and also for the efficacy of the control agent once released. Peak oviposition coincided with pods reaching maximum length, and seeds beginning to fill. Close synchrony between adult and emergence and the presence of susceptible pods will be critical to achieving high levels of seed destruction. Lack of synchrony may be the reason why infestation rate was low at several sites in New Zealand.

There is a tight requirement for synchrony between adult emergence and the presence of susceptible pods on trees, and any *Acacia* species that sets pods outside that period should be safe from attack. This further limits the likelihood that *B. acaciae* will affect African acacias. Kluge (1989) drew similar conclusions from his study of a *Bruchophagus* sp. reared from *A. longifolia* in Australia.

Adults have a short oviposition period each year. Timing host-range tests correctly would therefore be difficult. Further assessment of risk to African acacias should incorporate an analysis of seeding phenology of possible hosts. Although African acacias are rare in New Zealand gardens, it is likely that some grow and set seeds in Australia. Monitoring the seed-feeding fauna of exotic acacias in Australia, as this study did in New Zealand would more powerfully predict the likely host-range of *B. acaciae* in South Africa than unreliable field experiments, or tests in secure containment which would be impracticable.

Can *Bruchophagus acaciae* contribute to the biological control of acacias in South Africa? Seed-feeders can enhance integrated control of weeds in the short term by reducing invasion of new areas, or in the long term by exhausting seed banks to the point where recruitment of seedlings falls below replacement. Without some knowledge of the popu-

lation dynamics of acacias in South Africa, it is difficult to make firm predictions of its value, however, Shea (1996), and Rees and Paynter (1997) have shown that even moderate levels of seed destruction can theoretically lead to the decline of weed populations. The highest level of seed destruction recorded in this study was 95.6%, but it is more instructive to examine the average rate of infestation, and the variation between samples. Firstly, the rate of infestation of A. decurrens was always relatively low, which suggests that seeds of this species will not be effectively destroyed in South Africa by B. acaciae from New Zealand. The rank order of infestation rates of other acacias at particular sites was similar in both years (for example, "Junville" provided the lowest rates of infestation in both years). This suggests that some sites are inherently more suitable for this control agent than others. Infestation rates varied at the same sites between years, suggesting that even if rates are sometimes high, seed may "escape" in large numbers in some years, producing patchy control over time. For plants with long-lived seeds, occasional recharging of the seed bank in this way may limit the potential of B. acaciae to suppress the population. The mechanisms behind this variation were not examined. However, the data suggest that synchrony between adult emergence and the presence of pods that are suitable for oviposition is critical to the final level of seed destruction. Failure of this synchrony at the between-tree, between-site, or between-year level would strongly influence the impact of this agent on seed production.

It is likely that *Bruchophagus acaciae* was introduced to New Zealand in seed for sowing. However, it is not known when, or how often it was introduced, from where in Australia it originated, or from which *Acacia* species. Acacia seeds were presumably often imported to of New Zealand during the last century. If *B. acaciae* is not present in the North Island, it may be that successful colonisation by *B. acaciae* was rare, or happened only once. If so, the genetic variability present in New Zealand may be limited, and this may account for the observed behavioural characteristics of the eurytomid in New Zealand, for example the short emergence and oviposition periods, and the pattern of host-specificity. The genetic variability in New Zealand *B. acacia* merits further study. It may be possible to enhance the performance of this species in South Africa by augmenting New Zealand stock with a range of genetic material from Australia.

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