Thirty years of exploration for and selection of a succession of *Melanterius* weevil species for biological control of invasive Australian acacias in South Africa: should we have done anything differently?

F.A.C. Impson¹,² and V.C. Moran¹

Summary

The question of how we can be simpler, faster and better in exploring for and selecting successful agents for weed biological control has been on the agenda since these Symposia began. We give a brief account of the development of some of these ideas on how to “pick a winner”. For about 30 years, South African scientists have made exploratory trips to Australia to select agents for release against various alien acacias, and the related *Paraserianthes lophantha*. Besides two species of gall-forming wasps, a rust fungus, and far more recently, a cecidomyiid pod-galler, five seed-feeding *Melanterius* weevil species were chosen, and have proved to be highly successful. *Melanterius ventralis* was released against *Acacia longifolia* (in 1985); *M. acaciae* on *A. melanoxylon* (1986); *M. servulus* on *P. lophantha* (1989); *M. servulus* on *A. cyclops* (1991); *M. maculatus* on *A. mearnsii* (1994), and on *A. dealbata* and *A. decurrens* (2001); and *M. compactus* against *A. saligna* (also in 2001). With reference to this singular group of weevils, the question is, in retrospect, whether we should or could have done anything differently? The basic ingredients for success in exploration and selection still require that the agents are available, amenable and appropriate (politically, climatically, and in their niche selection and ability to inflict critical damage), and that the agents must be acceptably host-specific, and sufficiently prolific and peripatetic. We conclude, as many others have before us, that successful agent selection is a serendipitous blend of biological and ecological knowledge, and pragmatic circumstances.

Keywords: biological control, invasive acacias, *Melanterius* weevils, seed-feeders, South Africa.

Introduction

Implicit in the title of this Symposium session (“Ecology in exploration and agent selection”) is the notion that a better understanding of the biology and population dynamics of prospective agents, and their target weeds, may allow the formulation of generalities and principles that would expedite the practice of biological control. That is, we would be able to choose the best agent(s) that would inflict maximal damage, and reduce population densities of the target weed in the shortest time. Biological control practitioners have surely been gnawing on this old bone since the practice began: the concern is that weed biological control is not quantitative enough, not sufficiently predictable, and thus not “scientific” enough (Huffaker 1976), and may be more of an art than a science (e.g. Harris 1976).

Having said that, however, it is also true that a number of ideas on how to optimize the selection of agents and their targets have been well entrenched in the literature for decades. Many of these concepts have

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been widely applied consciously or otherwise by weed biocontrol practitioners. Table 1 provides a summary of these main concepts, together with a list of key references in which these ideas are variously discussed as they apply to the selection of insect agents. The latter information is gleaned from a review of the full-length articles on insect-agent and target selection that have been published, since 1980, in the six *Proceedings of the V–X International Symposia on Biological Control of Weeds*. The fifth Symposium was taken as the starting point for this review because it was the first of the major Symposia at which 100 or more delegates attended.

By the mid-1980s, most of the concepts listed in Table 1 had already been formulated. The only apparently novel idea that sparked some debate was the hypothesis that evolutionary “new-associations” between potential agents and their host plants could profitably be exploited in weed biological control (see Table 1 and Hokkanen & Pimentel 1984, Dennill & Moran 1988). However, even that idea was not really recent or novel – Room had already mooted it formally in 1981. Indeed, the “new-associations” concept must have been accepted even during the earliest days of weed biological control when *Cactoblastis cactorum* and cochineal insects were deployed as agents against *Opuntia* weed species (see Moran & Zimmermann 1984, and the critique by Goeden & Kok 1986).

We discuss achievements by entomologists over the years in their exploration for and selection of agents that have been used for the biological control of invasive Australian acacias in South Africa. One species of rust fungus, *Uromycladium tepperanium* has been spectacularly successful against *Acacia saligna* in South Africa (Morris 1999). But in this paper, the emphasis is on insect agents, and particularly on a group of seed-destroying weevils in the genus *Melanterius*. We review the history of these introductions and ask whether we could have or should have done anything differently to improve the levels of seed destruction achieved.

The history of exploration for and selection of insect species for the biological control of *Acacia* species in South Africa

The exploration for natural enemies of Australian *Acacia* species that had become invasive in South Africa began some 30 years ago (Neser & Annecke 1973, Van den Berg 1973, 1977, 1980a,b,c,d, 1982a,b,c). Thorough surveys were carried out, in Australia, (mainly by Drs S. Neser and M. Van den Berg) to discover as many natural enemies as possible. From the outset, the economic importance to South Africa of several of the Australian *Acacia* species was a crucial consideration in the selection of agents. The focus was on agents that would reduce the reproductive capabilities of the plants, but which would not otherwise damage the commercially important (albeit invasive) Australian species in South Africa (Dennill & Donnelly 1991). In this context, seed-attacking agents were recommended and given preference because of their tendency to be host-specific (Janzen 1971, 1975, Annecke 1978).

From long lists of natural enemies (Van den Berg 1980a,b,c, 1982a,b,c), a number of potential agents were proposed, amongst which were *Trichilogaster* species (Hymenoptera: Pteromalidae), *Bruchophagus* species (Hymenoptera: Eurytomidae) and *Melanterius* species (Coleoptera: Curculionidae) (Van den Berg 1977, 1980d), as well as the mirid bug, *Rayeria* sp., (which was rejected because it was not host-specific), Cecidomyiid flies and eriophyiid mites. Further consideration of the cecidomyiids and eriophyiids was shelved very early on due to a lack of knowledge regarding their taxonomy, biology and host ranges and also because of the lack of financial support and properly qualified people to work on additional agents (S. Neser, pers. comm. 2003). Cecidomyiids have recently been studied in earnest for use against several of the Australian *Acacia* species (Adair 2000, 2002), and *Dasineura dielsii* is now widely established on *A. cyclops* in South Africa.

*Bruchophagus* species were imported into quarantine in South Africa on several occasions during the 1980s (Kluge 1989) and more recently, but were never released for biological control of any of the Australian acacias. They are far less readily available on acacias in Australia than the *Melanterius* species; there are still questions about the taxonomy of the group (New 1983); and there are almost insurmountable technical difficulties in rearing the insects and in proving their host specificity. Thus, the focus of attention in the early years of the biocontrol program against Australian acacias was on the *Trichilogaster* and *Melanterius* species.

It was initially believed that seed-destroying agents would be acceptable to all stakeholders (including the owners of black wattle plantations – *A. mearnsii* – in South Africa) because they would be able to slow the reproduction of the invasive target plants while not destroying their useful attributes. However, serious concerns were raised by the wattle industry (Stubbings 1977), at a stage when exploratory surveys were well under way in Australia. These concerns hampered the progress and implementation of biological control for some years. The issue was apparently resolved and, in 1982, the biological control of Australian acacias in South Africa began with the release of the bud-galling wasp *T. acaciaelongifolii* on long-leaved wattle, *A. longifolia*, and with concerted efforts to collect and import *M. ventralis* (Dennill & Donnelly 1991). The bud-galling wasp established throughout the range of *A. longifolia* and drastically reduced the reproductive potential of its host plant (Dennill 1985, 1988, 1990, Neser 1985).
Before the success of *T. acaciaelongifoliae* had been properly evaluated, however, *M. ventralis* was released in 1985 (Dennill & Donnelly 1991). The weevils readily established at all release sites. Although populations were slow to increase, levels of seed destruction ranged from 14.9% to 79.5% after only three years (Dennill & Donnelly 1991). The weevils were particularly useful in destroying the seeds on *A. longifolia* plants growing close to rivers, where, despite the dramatic effects of *T. acaciaelongifoliae*, trees were able to produce many more pods per branch than in the drier areas (Dennill et al. 1999).

Even though *T. acaciaelongifoliae* (in combination with *M. ventralis*) was clearly successful, other *Trichiologaster* species were not considered for acacia biocontrol for several years. There may be at least two reasons for this. Firstly, in 1985 and 1987, cohorts of *Trichiologaster* species had been introduced into quarantine from Australia to see whether establishment would occur on *Acacia pycnantha*, and the results did not look at all promising (Dennill & Gordon 1991). Secondly, it had always been very evident that *T. acaciaelongifoliae* galls were acting as a nutrient sink and were thus very damaging to *A. longifolia*. Galling by the wasps greatly

### Table 1

Optimizing target and agent selection in weed biological control using insects: how to “pick a winner”. A summary of the main concepts is given. Authors that have written on one or more of these aspects in the *Proceedings of the International Symposia on Biological Control of Weeds*, since 1980, are listed in chronological order. General key references, in which many of these concepts are reviewed, are given at the bottom of the table.

<table>
<thead>
<tr>
<th>Main concepts</th>
<th>Authors who comment on these concepts</th>
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<tr>
<td>7. Ensure climatic matching</td>
<td>Harris 1985, Room 1985</td>
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<tr>
<td>8. Identify “vacant niches” on the target plant, or the most vulnerable stage, or time for attack</td>
<td>De Loach 1981, Lawton 1985, Room 1985, Müller 1990, Pecora &amp; Dunn 1990</td>
</tr>
<tr>
<td>9. Determine the number and sequence of agent species to be released</td>
<td>Pecora &amp; Dunn 1990</td>
</tr>
<tr>
<td>10. Choose seed-destroying agents for early phases of program, or to minimize conflicts</td>
<td>De Loach 1981, Cloutier &amp; Watson 1990</td>
</tr>
<tr>
<td>11. Determine most vulnerable weeds and potentially successful agents from their “track record”, i.e. the evolutionary or historical record</td>
<td>Crawley 1990, Kovalev &amp; Zaitzev 1996</td>
</tr>
<tr>
<td>12. Consider agents that have “new associations” (in evolutionary terms) with the target weed</td>
<td>Room 1981, Ehler 1995</td>
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<td>14. Accept that the biological complexities, and other requirements, preclude the formulation of useful generalities and that “picking a winner” in weed biological control should be done on a case-by-case basis, relying on accumulated wisdom and on the intuition of the biologists concerned</td>
<td>Chaboudez &amp; Sheppard 1995, Cullen 1995, Ehler 1995</td>
</tr>
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- Harris 1985, Room 1985
- Pecora & Dunn 1990
- De Loach 1981, Cloutier & Watson 1990
- Crawley 1990, Kovalev & Zaitzev 1996
- Room 1981, Ehler 1995
inhibits reproductive and vegetative growth, and causes branches and whole trees to collapse under the weight of galls, features that would have alarmed commercial wattle growers who perceived their industry to be under threat. Irrespective of these fears, a second Trichilogaster species was later established on the invasive, non-beneficial Acacia pycnantha in 1995 (Hoffmann et al. 2002).

Buoyed by the ready establishment of M. ventralis in 1985, the following years were dominated by research on the Melanterius group of weevils. In 1986, a second weevil species, M. acaciae, was released on A. melanoxylon (Dennill & Donnelly 1991). Conflicts with commercial wattle growers arose yet again in 1987 with the pending release of M. servulus for the biological control of the Australian Paraserianthes lophantha (a close relative of the acacias). Quarantine testing had demonstrated that M. servulus could also oviposit and develop within seeds of A. mearnsii (Donnelly 1992). This was an obvious concern, but despite earlier agreements with the wattle industry regarding acceptable levels of seed damage, the release was opposed. The program was suspended temporarily, but a compromise was later reached, in 1989, when it could be proven that A. mearnsii seeds in orchards could be chemically protected from the weevils (Donnelly et al. 1992). Melanterius servulus was then cleared for release. Shortly after this, in 1991, M. servulus was also released onto A. cyclops. Eventually, in 1993, the first releases of M. maculatus were made on A. mearnsii, which was the mainstay of the wattle industry and the subject of most of the conflict over the years. Although initial releases of M. maculatus were restricted to the Western Cape Province, release of this species has now been extended to cover much of the country. More recently (in 2001), M. maculatus was also introduced onto two closely related wattles, A. dealbata and A. decurrens. Lastly, but also in 2001, a fifth weevil species, M. compactus, was introduced and established on A. saligna (to supplement the action of the rust fungus U. tepperanium).

**The Melanterius seed-feeding weevils used for biological control in South Africa**

To date, some 88 species of Melanterius have been described (R. Oberprieler, pers. comm. 2002). This large group of curculionid weevils is, for the most part, native to Australia, and appears to be associated exclusively with Australian Acacia species (Auld 1983, New 1983, Donnelly 1992). The Melanterius species used in South Africa are small (3–5 mm), univoltine weevils, that breed in spring, coinciding with the peak period of pod production of their acacia hosts. Adult weevils feed mainly on green, developing seeds during this time, and to a lesser extent, at other times of the year, on buds, flowers, new vegetative growth and young pods. Mating and oviposition follow the spring feeding. The female weevils chew small holes through the walls of the swollen green pods, through which they insert a single egg. The eggs are placed onto, or near, the developing seeds. The newly hatched larvae burrow into the seeds, where they feed and complete their larval development. Generally only one larva develops per seed, during which time the entire contents of the seed are consumed, leaving the hard outer coat. (In some Melanterius species, a single larva may devour more than one seed.) Fully developed larvae then chew their way out of the pods, and drop to the ground and pupate in the soil. Some larvae remain in the soil until the following breeding season, but most of the adult weevils emerge from the soil 6–8 weeks later. These adults remain mostly inactive for the cooler months, sheltering under the bark of their host or other plants in the vicinity, and only become evident in large numbers again during the next spring.

Although Melanterius species each seem to be specific to a very narrow range of Acacia species, the host-plant and phylogenetic relationships of Australian acacias and their Melanterius weevils are poorly understood. Certainly some patterns of host association are evident. For example, M. ventralis, which is morphologically and phylogenetically distant from other Melanterius species used for biocontrol in South Africa (Clarke 2002), is specific to A. longifolia, the only target species belonging to the section Juliflorae in the genus Acacia. In the less specific M. maculatus, the main hosts (A. mearnsii, A. dealbata, A. decurrens and A. baileyana) all belong to the section Botrycephalae (Oberprieler & Zimmerman 2001). Such associations in Melanterius can be accurately determined only from a comprehensive and detailed study of specimens reared through from seeds or pods of the actual host plant. Adult Melanterius weevils that are found on various Acacia species in Australia (where they sheltering under bark or in the canopy) can create incorrect assumptions about host-plant relationships.

Much of the recent evaluation on the impact of Melanterius species on acacias has been on M. servulus on A. cyclops (Impson et al. 2000). Evaluations have also been done on P. lophantha (Schmidt et al. 1999), A. mearnsii (F. Impson, unpublished data), A. longifolia (Dennill & Donnelly 1991) and A. melanoxylon (Donnelly 1995). Seed destruction is the combined consequence of Melanterius feeding, ovipositional activities, and larval development. From the data accumulated thus far, it seems that the various Melanterius species have similar impacts on their different acacia hosts in South Africa, so it is possible to generalize about what can be expected and achieved from biological control efforts using these agents.

Early records of M. ventralis on A. longifolia, and of M. acaciae on A. melanoxylon, indicate slowly increasing levels of seed damage over several years,
followed by gradual dispersal of the weevils away from the release sites (Dennill & Donnelly 1991, Donnelly 1995). *Melanterius servulus* on *A. cyclops* shows the same pattern. Although the weevils cause negligible damage to the buds and immature pods, the greatest damage to the host plant is that inflicted on the almost-mature green seeds. Following release of the weevils, gradual increases in seed damage were recorded, from only 7% to 95% at some sites, after approximately five years (Impson *et al.* 2000). Seed destruction by the weevils is unlikely to result in a reduction in the density of the target plants because this requires consistently high levels of seed mortality, i.e. >99%. However, seed destruction is a substantial aid to management of these invasive trees, a matter that is more fully discussed by Moran, Hoffmann & Ockers in a separate contribution in these Symposium Proceedings.

Several factors play a role in the levels of seed destruction achieved (e.g. fires and manual clearing), and the rate of build-up is also affected by the initial numbers of weevils released at a site, the relative seed abundance, and the rate of weevil dispersal. Dispersal rates of *Melanterius* species are relatively slow (approximately 2 km per year; F. Impson, unpublished data). However, *Melanterius* species are easy to redistribute manually, which substantially increases their effectiveness.

**Discussion and conclusions**

It is instructive to review 30 years of effort in the biological control of Australian acacias that have become invasive in South Africa, and to question whether these efforts could have been more effective. It would be trite to note that more time and money could have been expended in collecting more *Melanterius* weevils, and other agents, more widely and more often. Bearing in mind that much of the information from the literature (e.g. Table 1) was not available in the 1970s, the question is whether there are some aspects from these “guidelines” for exploration and selection of biocontrol agents that were omitted or ignored and which, if now implemented, could improve the levels of seed destruction that have been achieved. The answer is probably not.

In retrospect, the past emphasis on *Melanterius* weevils seems obvious and appropriate. They are sufficiently, but not always completely, host-specific (they do not feed on or oviposit in any native acacias in South Africa or on any other plants). They were readily available, in that South African scientists were allowed access to Australia, and the weevils were relatively easy to collect. In addition, earlier biological control program in South Africa using seed-feeding weevils (*Erytenna consputa* on *Hakea sericea*; see Kluge & Neson 1991) had set a favourable precedent for the use of these types of agents. As seed-destroying agents, *Melanterius* weevils were grudgingly eventually accepted by commercial growers of Australian acacias (mainly *A. mearnsii*) in South Africa, as suitable for importation. The weevils had no difficulty adapting to the climate in their country of introduction and they have built up hugely in numbers over the years. The successes that have been achieved are largely a tribute to the skills, knowledge and intuition of the naturalists who were given the initial task of exploring for and selecting agents for acacia biocontrol in South Africa, more than 30 years ago (in particular, Drs S. Neson and M. Van den Berg).

This review of the literature on insect-agent and target selection in weed biological control suggests two realities. (i) There is acceptance that non-biological, extraneous factors, such as political pressures, permits, transport difficulties, funding etc. may dominate in the exploration for and selection of agents. (ii) There is also widespread acknowledgement that, while the checklist of concepts listed in Table 1 represents an essential starting point, the reality of selecting insect agents in the field has to be determined on a case-by-case basis, and will seemingly always rely on a serendipitous blend of biological and ecological knowledge, and pragmatic circumstances.

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**References**


Selection of *Melanterius* spp. for acacia control


