Multiple-species introductions of biological control agents against weeds: look before you leap

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Summary

Biological control practitioners have frequently debated the issues behind single vs multiple species introductions against target weeds. In the case of weed biological control, conventional wisdom is that multiple species should be used on the assumption that several species are more likely to have a greater controlling impact than a single species alone. This debate is rehearsed with reference to the biological control of four species of Australian acacias in South Africa: long-leaved wattle (Acacia longifolia (Andr.) Willd.), golden wattle (Acacia pycnantha Benth.), Port Jackson willow (Acacia saligna (Labill.) H. Wendl.) and rooikrans (Acacia cyclops A. Cunn. ex G. Don), where the impacts of both gall-forming and seed-reducing agents were intended to be additive and possibly synergistic. Evaluation and observations of these specific cases show that multiple-species introductions can be beneficial, but in at least one case (A. cyclops), the wisdom of these releases is questionable and potentially even detrimental. This suggests the need for extreme caution when planning multiple-species introductions against a target weed species.

Keywords: multiple species, Acacia, biological control.

Introduction

For many years, biological control practitioners have discussed and debated the merits of releasing multiple as opposed to single species of biological control agents in weed control programmes. The focus of such discussion has been multifaceted, either in terms of the effectiveness of the actual control (Myers, 1985; Myres et al., 1989; Story et al., 1991; Müller-Schüerer and Schroeder, 1993; Hoffmann and Moran, 1998; Anderson et al., 2000), competitive interactions between agents (Zwölfer, 1973; Ehler and Hall, 1982; Denno et al., 1995; Woodburn, 1996; Briese, 1997; McEvoy and Coombs, 2000), the best timing or sequence in which to introduce agents (Briese, 1991; Syrett et al., 1996), or in terms of risk, safety and direct and indirect non-target effects (Myers, 1985; Simberloff and Stiling, 1996; Callaway et al., 1999; Denoth et al., 2002; Pearson and Callaway, 2005).

For most weed biological control projects, the highest levels of ‘success’ have been achieved using multiple agents, either because there has been a cumulative or synergistic effect of all agents working together (e.g. Hoffmann and Moran, 1998) or because as agent numbers are increased, there is likely to be a greater probability that the most suitable species will be released, often with a single agent being responsible for the success (Myers, 1985). Alternatively, the introduction of more agents may ultimately provide a higher probability of biological control over wider geographical ranges, due to different agent species performing better under different conditions (DeBach, 1964; Baars and Heystek, 2003; Day et al., 2003). In many cases, new and additional agents are released prematurely, either because existing agents have not been adequately evaluated or because agents have not been provided an opportunity to achieve their full potential (McFadyen, 1998; McEvoy and Coombs, 2000). Unfortunately, predicting the effectiveness of, and possible interactions between, potential biological control agents remains an
ongoing and daunting challenge (Cullen, 1995; Zalucki and van Klinken, 2006).

The biological control programmes against four invasive Australian Acacia species in South Africa are discussed with respect to these issues. They demonstrate that although multiple-agent releases are usually beneficial, there are times when this may not be the case and releases of more than one agent should be planned with caution.

Biological control of Acacia species in South Africa

During the last 30 years, biological control has been implemented against nine of the most invasive Australian Acacia species in South Africa (Dennill et al., 1999). Collectively, these programmes have largely been governed by conflicts of interest over desires to control the plants whilst continuing to exploit them commercially for production of tannin, for timber and pulp, for fire wood and for dune binding. Consequently, the choice of biological control agents has been restricted, for the most part, to agents that limit the reproductive output of their hosts, thereby reducing invasiveness but not the useful attributes of the plants. Four of these acacias have been subject to control by two agent species released sequentially (Table 1), and they are the subject of discussion here.

Acacia longifolia (Andr.) Willd. (long-leaved wattle): The gall-forming wasp, Trichilogaster acaciaelongifolii Froggatt (Hymenoptera: Ptormalidae), was released on A. longifolia in South Africa during 1982 (Dennill and Donnelly, 1991). The wasps dispersed readily and reduced seed production on A. longifolia by more than 95%, even causing some suppression of vegetative growth of the plants (Dennill, 1988). However, there were two situations where T. acaciaelongifolii was not fully effective: (a) in the hot, arid, inland areas and in the elevated, moist, mist-belt regions of the country where climatic conditions curb population expansion of the wasps (Dennill and Gordon, 1990) and (b) A. longifolia plants growing close to rivers do not suffer water stress and still produce substantial seed loads despite high levels of galling by the wasp (Dennill et al., 1999).

Although the impact of T. acaciaelongifolii was being studied, a second agent, a seed-feeding weevil, Melanterius ventralis Lea (Coleoptera: Curculionidae), had been proposed for control of A. longifolia and was being tested in quarantine. By 1985, the need for an additional agent was deemed to be necessary, and the first releases of M. ventralis were made. The seed-feeding weevils established readily at release sites and have subsequently played an important supplementary role in the suppression of seed production by A. longifolia (Dennill et al., 1999; Donnelly and Hoffmann, 2004).

Acacia pycnantha Benth. (golden wattle): Following the success of T. acaciaelongifolii on A. longifolia, a related species of gall-forming wasp, Trichilogaster signiventris (Girault) (Hymenoptera: Ptormalidae), was released against A. pycnantha during 1987. After a slow start, when it was believed that the wrong strain of T. signiventris may have been imported (Dennill and Gordon, 1991), and additional releases in 1992, levels of galling increased dramatically, and the insects became abundant throughout the range of A. pycnantha by 1998. Besides substantial reductions in seed production due to the wasps, in some cases, extensive galling caused collapse of branches and toppling of whole trees (Dennill et al., 1999; Hoffmann et al., 2002). Although initial indications were that no additional agents would be required to further reduce seed production, monitoring of pod and gall loads (in 2004 and 2005) demonstrated that many seed pods were still being produced despite the damage caused by T. signiventris.

The successful combination of the gall former and a seed feeder in the A. longifolia programme paved the way for a similar approach with A. pycnantha, and in 2005, the seed-feeding weevil, Melanterius maculatus Lea (Coleoptera: Curculionidae), was released. Although it is still too early to draw conclusions regarding the combined impact of the two agents, indications are that both agents will complement each other in reducing seed loads of A. pycnantha plants as is the case on A. longifolia.

Acacia saligna (Labill.) H. Wendl. (Port Jackson willow): Biological control of A. saligna had been recommended as a priority from the outset of the programme against the Australian acacias (Neser and Annecke, 1973). The gall-forming rust fungus, Uromycladium tepperianum (Sacc.) McAlp. (Uredinales: Rovene- liaceae), was selected as being a suitably damaging agent in that it could reduce reproductive output and also weaken the plants and ultimately cause their death (van den Berg, 1977). After its release in 1987, U. tepperianum rapidly dispersed throughout the range of A. saligna. Long-term evaluation studies demonstrated that the rust was an extremely effective agent, reducing population densities of adult trees by up to 85% (Wood and Morris, 2007). However, as in the case of A. longifolia and A. pycnantha, A. saligna was still able to produce large seed loads before succumbing to the effects of high levels of galling.

Again, the need was recognized for a second agent to target the remaining seeds, and another seed-feeding weevil, Melanterius compactus Lea (Coleoptera: Curculionidae), was released against A. saligna in 2001. Although the introduction of M. compactus is relatively recent, preliminary monitoring indicates that, like its counterpart on A. longifolia, the weevils are playing an important supplementary role in curbing the production of viable seeds on A. saligna.

Acacia cyclops A. Cunn. ex G. Don (rooikrans): A. cyclops was the last of the four species under discussion to be subjected to biological control. In the early 1990s, there was a strong focus on the Melanterius
group of weevils, which were readily available and easy to collect and had been shown to be sufficiently host-specific and damaging to warrant consideration (Impson and Moran, 2004). In 1991, the first release of *Melanterius servulus* (Pascoe) (Coleoptera: Curculionidae) was carried out, followed in 1993 by more widespread releases. Although the weevils established successfully, they were relatively slow to build up their populations, and dispersal was also limited (Impson et al., 2004; Impson, 2005). Despite this, levels of seed damage increased with time at many of the release sites, with up to 95% seed damage being recorded within 5 years of release at some of the sites. Manual redistribution has been used to compensate for slow rates of natural dispersal.

In 2001, a proposal was made that a second agent, a flower-galling midge, *Dasineura dielsi* Rübsaamen (Diptera: Cecidomyiidae), should be released to supplement the activities of *M. servulus*. It was anticipated that the midge would fulfill a complementary role and have good dispersal abilities, which would thus compensate for the problem of slow dispersal rates of the weevil. At the time, some concerns were expressed regarding possible competitive interactions between the two control agents (i.e. by galling the flowers, the midge would indirectly remove the food source of the weevils), but the matter of containing large invasions of *A. cyclops* was considered a priority and additional restrictive measures against this plant were strongly supported.

Following the establishment of *D. dielsi*, the midge dispersed extremely rapidly (hundreds of kilometers per year) throughout the range of *A. cyclops* (J. Moore, personal communication, 2003), and with its multivoltine life cycle, populations of the midge exploded. It initially appeared that the proverbial 'silver bullet' had been released, and *A. cyclops* trees had been all but sterilized by the extremely high levels of galling. However, this situation did not persist, and midge populations have become less stable, resulting in considerable variation in the amount of pod set between sites and between years (F. Impson, C. Kleinjan and J. Moore, unpublished results). This has obvious implications for *M. servulus* because the weevils may no longer be able to sustain their populations when faced with an unpredictable food source, and ultimately, the success of the biological control programme against *A. cyclops* may be compromised.

**Discussion**

In these four cases of biological control against imported Australian acacias, there was a clear rationale, based on available knowledge, which governed the pattern and sequence of the releases of agents (Table 1), and in each case, the release of two agents has been justified.

For each of *A. longifolia*, *A. pycnantha* and *A. saligna*, a gall-forming agent was released before being followed up by a seed-destroying weevil (Table 1). In all of these programmes, the sequence of releases (i.e. a gall former preceding a seed feeder) was largely determined by opportunistic and pragmatic considerations. Agents that were readily available, obviously damaging to the host plant, abundant and easy to collect and amenable to specificity testing enjoyed priority. In the case of *A. longifolia*, the release of two species of agents occurred within 3 years of each other, and it is possible that if practical circumstances had been different the order of release could have been reversed. The cases of *A. pycnantha* and *A. saligna*, respectively, are different in the sense that considerable time elapsed between the releases of the first and second agents. The reason for this was a conscious decision to evaluate the impact of the gall formers acting on their own, before taking the decision to release a supplementary agent. In both cases, events were to prove that although the gall formers were highly effective, there were more than sufficient seeds left in the system to maintain populations of the host plants at problematic levels. There was a clear need for the seed-feeding weevils to reduce the numbers of viable seeds.

The pattern for *A. cyclops*, however, is different in that a seed-feeding weevil species was released first, followed several years later by the release of a gall midge. Again the sequence of release was determined by pragmatic and opportunistic circumstances and was influenced by strong demands for additional control measures against *A. cyclops*, particularly in view of the slow dispersal rates of *M. servulus*. The, gall midge, *D. dielsi*, was not an obvious choice of agent, primarily because of doubts about the effectiveness of gall midges as biological control agents (Goeden and Louda, 1976; McFadyen, 1985; Wehling and Piper, 1988; Carlson and Mundal, 1990; Harris and Shorthouse, 1996) and because from the outset there were some concerns over a potential conflict with *M. servulus*. Eight years elapsed before it was decided that a supplementary agent was needed.

The *A. cyclops* programme differs from the others in one other important respect. In the case of *A. longifolia*, *A. pycnantha* and *A. saligna*, the gall-forming agents are essentially univoltine, exert pressure on the plants and substantially reduce seed production, but in most circumstances, there are sufficient seeds remaining locally or in a wider area to sustain populations of the seed-feeding weevils. In other words, the evidence suggests that the effects of the agents are complementary. The gall-forming cecidomyiids, *D. dielsi*, on *A. cyclops*, by contrast, goes through several generations a year, most of which coincide with the peak flowering period of the plant (the females lay their eggs in the flowers), which initially led to enormous gall loads and the virtual or complete elimination of pods at sites. Subsequently, levels of pod production have been extremely variable. Of concern is the possibility that the fluctuations in pod set will destabilize populations of *M. servulus* and render the beetles unable to exploit and
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Table 1. The four species of Australian acacias targeted for biological control in South Africa, using in each case sequential releases of two agent species, all imported from Australia. In certain cases (marked by asterisk), there were previous releases, but they were unsuccessful.

<table>
<thead>
<tr>
<th>Acacia species (Mimosaceae)</th>
<th>Agent released</th>
<th>Date of first release</th>
<th>Release interval between agents (years)</th>
<th>Mode of action</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. A. longifolia (long-leaved wattle)</td>
<td>1. Trichilogaster acaciaelongifoliae</td>
<td>1982</td>
<td>3</td>
<td>Induces extensive gall formation</td>
<td>Dennill, 1988; Dennill and Donnelly, 1991</td>
</tr>
<tr>
<td>2. M. maculatus</td>
<td>2005</td>
<td>Destroys seed</td>
<td>F. Impson, unpublished results</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. A. saligna (Port Jackson willow)</td>
<td>1. Uromycladium tepperianum</td>
<td>1987</td>
<td>14</td>
<td>Induces fungal galls on reproductive and vegetative tissue</td>
<td>Morris, 1991</td>
</tr>
<tr>
<td>2. M. compactus</td>
<td>2001</td>
<td>Destroys seed</td>
<td>F. Impson, unpublished results</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. A. cyclops (rooikrans)</td>
<td>1. M. servulus</td>
<td>1993*</td>
<td>8</td>
<td>Destroys seed</td>
<td>*Dennill et al., 1999; Impson, 2005</td>
</tr>
<tr>
<td>2. Dasineura dielsi</td>
<td>2001</td>
<td>Induces galling of flowers</td>
<td>Adair, 2004</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1.

M. servulus destroys the surfeit of seeds that develop when *D. dielsi* is less effective. At times when seeds are scarce, the situation is further exacerbated by rodent and bird predation of the seeds. The adult weevils also feed widely on the ripening seeds, leaving virtually no seeds that are in a suitable condition for oviposition. Under these conditions of extreme seed scarcity, the weevil populations are in danger of becoming extinct locally or even over wide areas.

It is still too early to predict the long-term outcome of this programme. Preliminary studies indicate that the unstable conditions over the last few years have impacted on *M. servulus* populations at some monitoring sites, and if this situation persists, it may prove to be inimical to the biological control programme against *A. cyclops* in the long term. Alternatively, midge populations may ultimately stabilize at levels where sufficient pods are consistently available at sites. Under such conditions, it is anticipated that *M. servulus* populations would build up again and that the actions of *D. dielsi* and *M. servulus* could be additive, as it is for the other *Acacia* species with two agents. In addition, the objective of harnessing the high dispersal abilities of *D. dielsi* would also have been realized.

Apart from the fact that the introduction of organisms contains inherent risk, the broader ecological consequences of introductions have received little attention and remain poorly understood. Weed biological control is only contemplated in situations where mechanical and/or chemical control of invasive plants is impractical or prohibitively expensive. Predicting the outcome of introductions remains problematic because, frequently, the interacting attributes of the agent, the target weed and the environment are extremely complex. Furthermore, the introduction of each additional agent introduces another tier of complexity, complicating the ability to correctly predict outcomes.

In the case of the releases of a second agent onto *A. pycnantha* and *A. saligna*, sufficient time had elapsed between the introductions of the gall formers and the subsequent decision to release seed feeders; the impacts of the gall formers were well understood, and a clear need for an additional agent that would target residual seed production was identified. In addition, extensive knowledge of the attributes of *Mlanterius* spp. and their potential as biological control agents in South Africa was available. With *A. cyclops*, sufficient time had elapsed after the introduction of *M. servulus* for adequate evaluation of its performance and the recognition of its limitations. However, the ability to predict the outcome for the midge and its possible interactions with *M. servulus* was limited. The situation with *A. cyclops* in South Africa highlights the need for extreme caution when contemplating multiple species introductions and adds credence to the rule that biological control agents in any situation should only be introduced where circumstances demand and where the best predictions, as a result of experience, intuition or modeling, suggest that these multiple species introductions will not worsen the situation.
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