CRC for Australian Weed Management **#7**

Technical Series

Improving the selection, testing and evaluation of weed biological control agents

Editors: H. Spafford Jacob and D.T. Briese

CRC
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Improving the selection, testing and evaluation of weed biological control agents

Proceedings of the CRC for Australian Weed Management Biological Control of Weeds Symposium and Workshop

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Editors: H. Spafford Jacob and D.T. Briese

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Front cover: *Larinus latus* (Coleoptera: Curculionidae) a biological control agent released against *Onopordum* thistles in Australia.
Photo courtesy of David Briese.

Acknowledgments

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Preface

Putting more science into the art of biological control

Rick Roush

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For more than 30 years, discussions in learned scientific meetings have often fretted that the practice of classical biological control was more art than science, with heavy reliance on rules-of-thumb based on patterns of practice, but not on experiments. Classical biological control was inspired by the successful control of cottony cushion scale in California in the 1880s, when US government entomologist C. V. Riley recognised that the pest was native to Australia and New Zealand, and sent Walter Koebele to find and bring the scale's natural enemies back to California. Biological control workers have traditionally been outstanding naturalists and observers, but were often forced for reasons of limited funding to import anything that looked like it would do some good but wouldn't do any harm (Beirne, 1975). Thus, despite the enormous successes of classical biological control, and the influence of biocontrol and its researchers on the science of animal ecology, many of the key processes and research questions of biological control itself were not often studied until the last decade or so (for examples of such discussions, see Mackauer *et al*., 1990, Hopper *et al*., 1993, Hopper & Roush, 1993).

As reviewed by David Briese and colleagues in the introductory paper of this collection, there is now a much greater emphasis on trying to improve the efficiency of biological control (eg., through more rational choice of agents likely to be effective) and on reducing the chances of any adverse impacts of natural enemy introductions on native or desirable species. As with biological control more generally, Australia has made major contributions to these questions. Briese *et al*. note that Australian scientists have been leaders in weed biocontrol since undertaking the near legendary biocontrol of *Opuntia* cactus in the 1920s. I suggest that this is a tribute not only to the intellectual skills of Australian scientists, but also driven by necessity; Australia must depend on biological control to address many of its weed problems.

The vast size of Australia coupled with its low population density (especially outside the 5 major cities and away from the coast lines) means that weed problems of grazing lands and natural ecosystems, in particular, are far too large to be addressed by weed management tactics that require regular human inputs. For much of Australia, biological control is not just an environmentally friendly way to manage weeds and reduce pesticide inputs, it is the only practical way to reduce the ravages of exotic species of plants. In addition, the overall financial returns on investment for past projects have been excellent, even for the redistribution of agents (see CIE, 2001).

It was natural therefore that the Cooperative Research Centre for Australian Weed Management would place particular emphasis on biological control of weeds and organise a workshop to focus its research efforts on improving the science and practice of biological control. These papers discuss only a fraction of the CRC's work in biological control, but provide an introduction to the research that will continue Australia's world class contributions to general principles of biological control that can be applied to many other systems. This ranges from improving our understanding of how to conduct host specificity testing more efficiently and reliably (from David Briese and also Tony Willis and colleagues), to approaches and challenges for choosing "winner" agents more effectively in the first place (by Andy Sheppard and also Rachel McFadyen). Evaluation of the successes of biological control is critical not only to improving the practice of biological control, but also to persuading ever-strapped funding sources (who often forget how bad problems were before biocontrol) to stay the course and reinvest in new programs. Such evaluations are critical not only in biological and management terms (as discussed by Dhileepan and by Anthony Swirepik and Matthew Smyth) but also in the economic terms that, by necessity, form the bottom line for decision makers. Tom Nordblom has advanced this case both in his paper here and in his work on the economics of biocontrol of Paterson's curse for the Weeds CRC (CIE, 2001). Ecological models are increasingly being used for both prediction of the impact of biological control as well as in evaluating its successes, as illustrated by Darren Kriticos.

In sum, this excellent collection of papers shows that Australian weed scientists have their eyes clearly set on the key questions raised both by scientists and other stakeholders. Answers to these questions will never be absolute, but with this start will surely improve over the next five years, and beyond.

Preface references

Beirne, B. P. (1975) Biological control attempts by introductions. *Canadian Entomologist* **107**, 225-236.

Centre for International Economics (2001) The CRC for Weed Management Systems: An impact assessment. *CRC for Weed Management Systems Technical Series No. 6*, 42 pp. (also at http://www.weeds.crc.org.au)

Hopper, K. R., Roush, R.T. & Powell, W. (1993) Management of genetics of biological-control introductions. *Annual Review of Entomology* **38**, 27-51.

Hopper, K. R., & Roush, R. T. (1993) Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology* **18**, 321-331.

Mackauer, M., Ehler, L.E. & Rollands, J. (1990) *Critical Issues in Biological Control*. Intercept, London.

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The selection, testing and evaluation of weed biological control agents: Is there still room for improvement?

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Summary

The recently formed Cooperative Research Centre for Australian Weed Management now comprises almost all researchers in Australia who work on the classical biological control of weeds. This workshop was organised by the CRC to take stock of recent Australian research in biological control of interest to it and to suggest how the CRC can address key areas of concern for weed biological control; namely, the selection of biological control agents, agent host-specificity determination and the evaluation of agent impact. The workshop was arranged around a set of issues papers for each area, followed by discussions held amongst the workshop participants aimed at informing the research agenda of the new CRC and developing a common approach to the discipline in Australia. The issues papers and syntheses of the discussions held and recommendations made are contained in these proceedings.

Key words: biological control, weeds, biocontrol agent selection, host-specificity, biocontrol agent evaluation

Australian scientists have been at the vanguard of weed biological control since the 1920s when the control of *Opuntia* spp. cacti created a landmark example of successful control that is still used today. Since then, the science underpinning biological control has evolved enormously, and the practice of weed biological control has improved along with this. However, there are still some critical issues at the heart of the practice that need to be addressed to the satisfaction of practitioners, policy-makers and the general public.

Views on biological control always distil down to two issues: safety and effectiveness. It is not a trivial thing to deliberately introduce exotic organisms into a new environment (see Ewell *et al*., 1999) and, currently, there is considerable debate on the risks, ethics and value of biological control (e.g. Simberloff & Stiling, 1996; Waage, 2000; Strong & Pemberton, 2000). We are therefore accountable, not only to funding bodies, but to future generations and to the scientific discipline to ensure that the selection and release of agents is a both a good ecological and financial investment. As biological control practitioners, we need not only to get it right, but to show that we have gotten it right, and we can only do this if our science is sound. Hence, every so often, it is useful to take stock of where we are in relationship to current ecological theory and understanding. Are we still using best practice to ensure that weed biological control is as safe and effective as it can be?

The initiation of the Cooperative Research Centre (CRC) program has helped created a framework for the better implementation of weed biological control and, in particular, has helped place it in the context of overall weed management strategies (Briese, 2001). The establishment of the CRC for Australian Weed Management (CRCAWM) in 2001 brings together, under one banner, almost all researchers currently working in Australia on classical weed biological control. As such, it provides an unparalleled opportunity to look at the way we have been conducting our discipline, to seek a better understanding of the scientific framework for it and to improve our practices and success rates (see Briese 2001).

From a biological control perspective, CRCAWM has had two more regionally-focussed predecessors. From 1992 to 1999, the CRC for Tropical Pest Management developed techniques for evaluating the impact of agents on parthenium (Dhileepan, 2001) and water hyacinth (Heard & Winterton, 2000) in northern Australia and undertook work to improve the methodology of host-specificity testing (e.g. Withers *et al*., 1999). During 1995 - 2001, the CRC for Weed Management Systems focussed on the biological control of key weed species in temperate Australia, with a strong emphasis on initiating new projects, the delivery of biological control to the end-users and the economic assessment of projects (Briese, 1999; CIE, 2001). During the course of this work, researchers were able to address several of the fundamental issues now of interest to CRCAWM (see Briese, 1999). This workshop provides the opportunity to pass the baton from the outgoing CRCs to the new CRC, by taking stock of their outcomes in weed biological control and determining how these can help shape the research agenda for CRCAWM.

CRCAWM has taken a more fundamental approach and has established a number of research tasks to specifically address those broader issues causing concern for weed biological control today. Three of these will be addressed in this workshop:

- the selection of biological control agents (how we prioritise particular agents for particular weeds or should we even try),
- host-specificity of control agents and how we can assess the risk to non-target species (are our testing protocols out of date and how safe are they?), and
- the evaluation of agent impact (developing methodologies for assessing the effect of agents on their target weed and measuring success).

These areas are particularly relevant today. There is still debate on whether a single ‘super-agent’ or a suite of complementary agents is more likely to achieve successful biological control (see Myers, 1985; Denoth *et al*., 2002) or whether more or fewer agent releases are desirable (e.g. McEvoy & Coombes, 1999). There is no agreement on how much science is needed to select biological control agents, yet to date only 70% of introduced agents have established in Australia and less than 25% contribute to control of the target weed (Briese, 2000). Given the general inadequacy of funding for biological control, consensus needs to be reached on the relative efficiencies, practicalities and chances of success of investing scarce resources into detailed pre-introduction studies to prioritise fewer agents or in post-introduction testing of larger numbers of agents.

These issues cannot be separated from safety consideration, given calls for more parsimonious selection of biological control agents to reduce the overall risk of non-target effects (McEvoy & Coombes, 1999). Indeed, there has been a gradual tightening of regulations and their interpretation by plant biosecurity and environmental protection authorities in Australia. Provision of information on non-target impact and demonstrated efficacy may well become issues in approving agents for release.

Inroads have been made into the methodology of host-specificity testing procedures (Withers *et al*., 1999; van Driesche *et al*., 2000). However, little has changed in the selection of test plant species to assess the risk of candidate agents since Wapshere (1974) proposed the centrifugal phylogenetic model, and there has been little debate on the issue. Is it still informative to test economically important but distantly related plants, the host plants of close relatives of the candidate agent or plants biochemically similar to but distantly related from the target weed (see Wapshere, 1974)? Significant advances in plant phylogeny and the understanding of host-choice evolution over the past 20 years make it timely to consider whether improvements to this model can be made that might increase testing efficiency and give more accurate assessments of risk to non-target species, Consensus on our approach to testing is needed to provide a clear and consistent message to those authorities charged with assessing the risk of introducing weed biological control agents.

Finally, the impacts of many weed biological control projects have not been adequately assessed. Historically, there has been a view that evaluation of biological weed control is an expensive luxury, because the classic successes are self-evident. However, lack of detailed impact assessment has led to poor definition of “partial” or “significant” success in weed biological control, and this has hindered accurate measurement of the full benefits of our science. Moreover, there is growing recognition that the benefits of projects may be enhanced through integration of biological control with other management strategies (e.g. Paynter *et al*., 2000; Huwer *et al*., 2002).

A related issue is the possibility of non-target impact by biological control agents in Australia. Greater attention to the documentation of any attack on non-target plants or indirect ecological effects will both allow the calibration of our risk assessment methodologies and reveal the safety record of biological control.

Evaluation is extremely important, given our accountability to funding providers and the general public, and the need to justify further investment in weed biological control, despite long time frames on the returns. The evaluation of biological control projects is a multi-tiered process, ranging from confirmation of agent establishment, through local and regional assessments of damage impact to full ex-post economic analyses (Syrett *et al*., 2000). However, development of the right tools (experimental approaches, survey techniques, modelling inputs) and a consistency of approach across projects are needed to provide more rigour and enable realistic assessments of the benefits of classical weed biological control. Much of the current debate on biological control practices and associated risks could be settled were appropriate impact data available.

In summary, we need to be clear why we choose agents, demonstrate that our testing protocols are state of art and give true indications of risk and demonstrate that we are capable of measuring impact, both on target plants and the ecological community. It is our hope that this workshop will be a starting point to a strong biological control research program by CRCAWM that will enable biological control practitioners to meet these goals in a consensual and systematic manner.

References

Briese, D.T. (1999) Enhancing biological control in temperate Australia through the CRC for Weed Management Systems. *Proceedings of the 12th Australian Weeds Conference* (eds T.J. Bishop, M. Boersman & C.D. Barnes), pp 229-234. Tasmanian Weed Society, Hobart.

Briese, D.T. (2000) Classical biological control. *Australian Weed Management Systems* (ed. B.M. Sindel), pp 161-192. Richardson Publ., Melbourne.

Briese, D.T. (2001) Creating a framework for the successful implementation of biological control. *Proceedings of the 3rd International Weed Science Congress*, MS No. 355, 12 pp, CD-ROM, International Weed Science Society, Oxford, MS.

Centre for International Economics (2001) The CRC for Weed Management Systems: An impact assessment. *CRC for Weed Management Systems Technical Series No. 6*, 42 pp.

Denoth, M., Frid, L. & Myers, J.H. (2002) Multiple agents in biological control: Improving the odds? *Biological Control* **24**, 20-30.

Dhileepan, K. (2001) Effectiveness of introduced biocontrol insects on the weed *Parthenium hysterophorus* (Asteraceae) in Australia. *Bulletin of Entomological Research* **91**, 167-176.

Ewel, J.J., O'Dowd, D.J., Bergelson, J., Daehler, C.C, D'Antonio, C.M., Gomez, L.D., Gordon, D.R., Hobbs, R.J., Holt, A., Hopper, K.R., Hughes, C.E., LaHart, M., Leakey, R.R.B., Lee, W.G., Loope, L.L., Lorence, D.H., Louda, S.M., Lugo, A.E., McEvoy, P.B., Richardson, D.M. & Vitousek, P.M. (1999) Deliberate introductions of species: Research needs - benefits can be reaped but risks are high. *Bioscience* **49**, 619-630.

Heard, T.A. & Winterton, S.L. (2000) Interactions between nutrient status and weevil herbivory in the biological control of water hyacinth. *Journal of Applied Ecology* **37**, 117-127.

Huwer, R.K., Neave, M.J., Dowling, P.M., Lonsdale, W.M., Sheppard, A.W., Briese, D.T. & Michalk, D.L. (2002) Integrated Weed Management (IWM) in perennial pasture using pasture and grazing management, herbicide strategies and biological control. *Proceedings of the 13th Australian Weeds Conference*, (eds H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 727-730. Plant Protection Society of Western Australia, Perth.

McEvoy, P.B. & Coombes, E.M. (1999) Biological control of plant invaders: Regional patterns, field experiments, and structured population models. *Ecological Applications* **9**, 387-401.

Myers, J.H. (1985) How many insect species are necessary for the biological control of weeds. *Proceedings of the 6th International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 377-382. Agriculture Canada, Ottawa.

Paynter, Q., Flanagan, G.J., Lonsdale, W.M., Schatz, T. & Steinbauer, M.J. (2000) Ecological studies to optimise the integrated management of the wetland weed, *Mimosa pigra*. *Proceedings of the 10th International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 389-395. Montana State University, Bozeman.

Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology* **77**, 1965-1974.

Strong, D.R. & Pemberton, R.W. (2000) Food webs, risks of alien enemies and reform of biological control. In *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp 57-79. CABI Publ., Wallingford.

Syrett, P., Briese, D.T. & Hoffmann, J. (2000) Success in biological control of terrestrial weeds by arthropods. In *Measures of Success in Biological Control* (eds S.D. Wratten & G. Gurr), pp 189-230. Kluwer, Amsterdam.

van Driesche R.G., Heard T. A., McClay, A. & Reardon, R. (2000) *Host-specificity testing of exotic arthropod biological control agents: The biological basis for improvement in safety*. Morgantown, USA. USDA Forest Health Technology Enterprise Team, FHTET-99-1.

Waage, J.K. (2000) Indirect ecological effects in biological control: The challenge and the opportunity. In *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp 1-12. CABI Publ., Wallingford.

Withers, T.M., Barton Browne, L. & Stanley, J. (1999) *Host Specificity Testing in Australasia: Towards Improved Assays for Biological Control*, Scientific Publishers, Indooroopilly.

Does ecology help in the selection of biocontrol agents?

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Summary

Increasing emphasis on actual and potential non-target effects is putting pressure on biocontrol workers to improve the selection methods for biocontrol agents, with the aim of reducing the number required to achieve successful control. An effective agent has to establish in the new country, and reach and maintain a sufficient population size to cause significant damage to critical stages of the target weed's life cycle. Knowledge of the ecology of the target weed and of the agent can help in the selection of effective agents, but the question is whether this is cost-effective compared to current prioritisation methods based on factors easily determined in the field.

Key words: biological control, weeds, agent selection, establishment success, success rates

Introduction

For most weeds that are biocontrol targets, there is a pool of host-specific insects and diseases present in the country of origin, all potentially available as biocontrol agents. This pool varies in size greatly, as few as 6 or 7 for rubber vine *Cryptostegia grandiflora* (Huwer & McFadyen, 1999) or 9 for purple loosestrife *Lythrum salicaria* (Blossey, 1995), but can be as large as the 441 species collected on *Mimosa pigra* in Central and South America (Harley *et al*., 1995). Lack of resources to test and import them all, and the increased potential for non-target effects from the release of numerous agents (Follett & Duan, 1999), mean there is pressure to select the "best" i.e. most effective agents to import first (McEvoy & Coombs, 1999; Louda *et al*., 2003). Recently, there has been increased attention to the ecology of the target weed, with the aim of identifying weak points where the impact of certain types of damage could significantly reduce the weed's population (Lonsdale *et al*., 1995; Edwards & Brown, 1997; Shea & Kelly, 1998). Knowledge of the ecology of the potential agent is also used to identify factors determining probable effectiveness in the new country. This paper discusses the issues involved in using knowledge of the target weed and agent ecology to predict actual post-release performance of a particular agent on a target weed in the new country, and in order to select the "best" agent for release.

Throughout, the presumption is that the agents considered are adequately host-specific for release in the target country. Host-specificity testing is a separate issue discussed in a paper by Briese (these proceedings).

Factors influencing success

Establishment

The first requirement for success is establishment of the agent in the new country. Methods to maximise successful establishment are the topic for another session, but there seems to be a small proportion of agents, between 10 and 20%, that still fail for unknown reasons despite best practice in mass rearing and release. We need to improve our ability to predict this failure if selection of agents is to improve, as an agent that fails to establish at all after detailed testing and considerable release effort is perhaps the greatest waste of resources. One possible cause in some previous programs has been mis-match between biotypes of the host plant in the native range and the target weed in its introduced range. That is, the agent was collected from a different biotype or sub-species of plant from the target weed. At one time, "new associations" of this kind were believed to increase the chances of success (Hokkanen & Pimentel, 1984) and many successful programs, from the control of the prickly pears with *Cactoblastis* onwards, resulted from agents collected from a plant different to the target weed (Julien & Griffiths, 1998). Nevertheless, there are other examples where insects collected from a different host plant biotype, fed on the target weed in laboratory cages, yet completely failed to establish in the field, and it is believed that adult oviposition choice may have been the reason (McFadyen, P.J., 1987a, b; McFadyen, R.E., 1985). That is, when confined in cages, the adult females oviposited on the target weed, or scattered their eggs around the cage, but in the field, the target weed does not provide the right stimulus to attract the females, and so establishment fails. Mis-match between agent collection plant biotype and target weed biotype was the cause of the failure of the first release of the rubber vine rust *Maravalia cryptostegiae* in 1994 (Evans & Tomley, 1996), and may have caused the failure to establish of the chrysomelid beetles introduced into Australia from Brazil for the control of groundsel bush *Baccharis halimifolia* (Julien & Griffiths, 1998). Where there is a difference, however slight, between the host plant and the target weed, it is very important to assess the female host selection (or with rusts, spore germination and development) in natural conditions, to determine if both plant biotypes are equally acceptable. Egg scattering behaviour can be an artefact of cage conditions, but can also be an indication that none of the plants present is an acceptable host for oviposition (Withers *et al*., 2000).

Impact on the weed

Once the agent has established and spread, impact on the target weed depends on the interaction of agent abundance and damage caused with the weed population ecology, in the new environment. The weed's population ecology can be studied in the target country, and the effects of different levels of damage on different life stages modelled (Lonsdale *et al*., 1995; Shea & Kelly, 1998). In practice, it is difficult to incorporate all factors such as competition from other plants particularly the crops, pastures, or competing native plants, on a weed which has suffered different levels of damage at different stages of growth. Extensive experimentation is necessary to model these effects and often even basic information, such as the size and persistence of the seed bank, and the role this plays in the weed's ecology, is not known prior to the start of a biocontrol program.

Potential damage caused by the agent to the target weed is usually well understood prior to agent release (Edwards & Brown, 1997; McFadyen & Weggler-Beaton, 2000). *Actual* impact of the damage on the weed's population is influenced by the magnitude, duration and timing of this damage, which is much harder to predict, as this depends on the agent's population size in the field throughout the year. Agent population size is affected by parasitism and predation, both very hard to predict (Hawkins, 1994; Hill & Hulley, 1995; McFadyen, 1997), as well as by factors such as the impact of climate (Dhileepan, 2001).

Current situation

The traditional approach is very well summed up by Blossey (1995) in his paper on the potential agents available in Europe for the control of purple loosestrife in the USA. He describes the various scoring systems proposed and their shortcomings. All were based on the ecology of the agent and its visible impact on the plant in its native range, and scored the different factors based on analyses of successful and unsuccessful agents in past programs. Blossey noted that the population ecology of the weed in the target country was an important factor but that information on this was lacking, as is normally the case. In practice, therefore, biocontrol scientists in the field selected agents (usually insects first) based on assessments of which caused most damage in the field and could be reared easily, and, of course, proved host specific. Harley *et al*. (1995) described this as "subjective assessments of the ability of a species to damage the weed" based largely on the visible damage in the field plus the individual scientist's past experience. In practical terms, this meant the obvious, wide-spread, abundant species were selected first.

To check the results achieved in this way, I extracted from Julien & Griffiths (1998) the numbers of agents introduced for all successful programs. My justification for using successful programs only is that the aim is to determine how many agents were introduced to achieve success, and with programs that are still unsuccessful, we cannot know if success is in fact achievable, whatever the selection method. Because my list is from Julien & Griffiths (1998), some programs may not be included, *e.g*. the recent stunningly successful control of the water weed, azolla, in South Africa with a single agent (McConnachie *et al*., 2000), and there may be others where success has been achieved since 1998. I have only used information for the first country of introduction, as the issue is selection between unknown and untried agents. Ecology may still be useful in the selection of proven agents, e.g. if an agent seemed promising in one continent but was heavily parasitised, it might be useful in another with a different parasitoid complex, or where failure was due to climatic extremes not present in another country.

The results are presented in Table 1, and the outcomes achieved were surprisingly good. In 32 programs, a total of 132 agents were introduced, 74% of which established and 55% of these contributed significantly to the successful control. In 24 of these programs, ranging from control of drooping tree pear in Queensland to Koster's curse in Fiji or black sage in Mauritius, success was achieved with only one, two or three agents established. In four programs, four or five agents were required, and only four programs had seven or more agents established – groundsel bush and prickly pear with seven, parthenium with nine and *Mimosa pigra* with ten. In all these successful programs, only one or two agents failed to establish, except in prickly pear and groundsel bush, where the cause was probably collection from the wrong host plant.

Table 1. The numbers of agents that failed to establish, established and contributed to the success of successful weed biological control projects (data from Julien & Griffiths 1998).

Weed	Country	Agents established	Agents failed to establish	Agents contributing to success
Acacia longifolia	South Africa	2	0	2
Acacia saligna	South Africa	1	0	1
Ageratina adenophora	Hawaii	1	1	1
Ageratina riparia	Hawaii	2	1	2
Alternanthera philoxeroides	Australia	2	1	1
Ambrosia artemisiifolia	Australia	3	1	2
Baccharis halimifolia	Australia	7	7	3
Carduus nutans	Mainland USA	2	2	2
Carduus spp.	Australia	1	1	1
Chondrilla juncea	Indonesia	3	1	1
Chromolaena odorata	Australia	2	1	2
Clidemia hirta	Fiji	1	0	1
Cordia macrostachya	Mauritius	2	1	2
Cryptostegia grandiflora	Australia	2	0	1
Eichhornia crassipes	Mainland USA	3	0	2
Emex spp.	Hawaii	3	2	1
Harrisia spp.	Australia	2	2	1
Hypericum perforatum	Mainland USA	5	1	2
Lythrum salicaria	Mainland USA	4	0	2
Mimosa invisa	Australia	1	1	1
Mimosa pigra	Australia	10	2	3
Opuntia aurantiaca	Australia	3	2	1
Opuntia stricta	Australia	7	4	1
Opuntia vulgaris	Australia	2	0	1
Parthenium hysterophorus	Australia	9	2	6
Pistia stratiotes	Australia	1	0	1
Salvinia molesta	Australia	2	0	1
Senecio jacobaea	Canada & USA	5	0	2
Sesbania punicea	South Africa	2	0	2
Sida acuta	Australia	2	0	1
Tribulus terrestris	Mainland USA	2	0	2
Xanthium occidentale	Australia	4	1	2
TOTALS: 38	**7 countries**	**98**	**34**	**54**

Role of ecology

The question is, can the use of ecology improve on the results being obtained by the traditional subjective method? In particular, can the greater understanding of the agent-weed interaction, based on detailed studies of the population ecology of the weed in the target country and of the impact of the agent in the native country, allow us to achieve successful control with the introduction of fewer agent species? For 75% of programs, success was achieved with three or fewer established agents, and only one or two which failed to establish. Will any feasible ecologically based method improve on this?

It is desirable to study the weed's population ecology in the target country because the information gained can be used to develop integrated management systems independent of biocontrol. The effects of different levels of damage on different life stages can then be modelled. In practice, it is difficult to incorporate all factors such as competition from other plants particularly the crops, pastures, or competing native plants, on a weed which has suffered different levels of damage at different stages of growth. Extensive experimentation is necessary to model these effects, and the issue for biocontrol practitioners is whether these ecological studies are the best use of scarce resources.

The aim is to develop predictive models for each weed to determine the critical stage of the weed's life cycle, such as root growth, or rapid recovery from storage organs after rain, or large seed production. Separate predictive models are then required to determine if a particular agent has the potential to inflict sufficient, appropriate and timely damage on the weed in the environment of the new country. These models can be validated against past programs where the results are known. At the same time, models should be developed for weeds currently the targets of biocontrol programs, so that the selection of new agents can be tested against the model predictions. Throughout, the challenge is to demonstrate that useful predictive models can be developed without the expenditure of enormous resources of time and money, which would otherwise be available for testing and importation of new agents.

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References

Blossey, B. (1995) A comparison of various approaches for evaluating potential biological control agents using insects on *Lythrum salicaria. Biological Control* **5**, 113-122.

Dhileepan, K. (2001) Effectiveness of introduced biocontrol insects on the weed *Parthenium hysterophorus* (Asteraceae) in Australia. *Bulletin of Entomological Research*, **91**, 167-176.

Edwards, P.B. & Brown, E.M. (1997) *Mesoclanis* seed flies (Diptera: Tephritidae) on *Chrysanthemoides* (Asteraceae) in South Africa: distribution, attack strategy and impact on seed production. *Bulletin of Entomological Research* **87**, 127-35.

Evans, H.C. & Tomley, A. J. (1996) Greenhouse and field evaluations of the rubber vine rust, *Maravalia cryptostegiae*, on Madagascan and Australian Asclepiadaceae. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J. H. Hoffmann), pp. 165-169. University of Cape Town, Stellenbosch.

Follett, P.A. & Duan, J.J. (1999) *Nontarget Effects of Biological Control*. Kluwer Academic, Boston.

Harley, K., Gillett, J., Winder, J., Forno, W., Segura, R., Miranda, H. & Kassulke, R. (1995) Natural enemies of *Mimosa pigra* and *M. berlandieri* (Mimosaceae) and prospects for biological control of *M. pigra. Environmental Entomology* **24**, 1664-1678.

Hawkins, B.A. (1994) *Pattern and Process in Host-Parasitoid Interactions*. Cambridge University Press, Cambridge.

Hill, M.P. & Hulley, P.E. (1995) Host-range extension by native parasitoids to weed biocontrol agents introduced to South Africa. *Biological Control* **5**, 287-302.

Hokkanen, H. & Pimentel, D. (1984) New approach for selecting biological control agents. *Canadian Entomologist* **116**, 1109-71.

Huwer, R.K. & McFadyen, R.E. (1999) Biology and host range of the hawk moth *Nephele densoi* Keferstein (Lep.: Sphingidae), a potential agent for the biological control of rubbervine *Cryptostegia grandiflora* R.Br. (Asclepiadaceae). *Biocontrol Science and Technology* **9**, 79-88.

Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds: a World Catalogue of Agents and their Target Weeds, 4th Edition*. CABI, Wallingford.

Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995) Biological control of a tropical weed: a population model and experiment for *Sida acuta. Journal of Applied Ecology* **32**, 391-9.

Louda, S.M, Pemberton, R.W., Johnson, M.T. & Follett, P.A. (2003) Nontarget effects - the Achilles heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review Entomol. 48, 365-96.

McConnachie, A.J., Byrne, M.J. & Hill, M.P. (2000) The successful biological control of the water fern *Azolla filiculoides* in South Africa. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), p. 427. Montana State University, Bozeman.

McFadyen, P.J. (1987a) Host specificity and biology of *Lioplacis elliptica* (Col.: Chrysomelidae) introduced into Australia for the biological control of *Baccharis halimifolia* (Compositae). *Entomophaga* **32**, 19-21.

McFadyen, P.J. (1987b) Host specificity of five *Anacassis* species (Col.: Chrysomelidae) introduced into Australia for the biological control of *Baccharis halimifolia* (Compositae). *Entomophaga* **32**, 377-9.

McFadyen, R.E. (1985) Larval characteristics of *Cactoblastis* spp. (Lepidoptera: Pyralidae) and the selection of species for biological control of prickly pears (*Opuntia* spp.). *Bulletin of Entomological Research* **75**, 159-68.

McFadyen,R.E. (1997) Parasitoids of the arctiid moth *Pareuchaetes pseudoinsulata* (Lep.: Arctiidae), an introduced biocontrol agent against the weed *Chromolaena odorata* (Asteraceae) in Asia and Africa. *Entomophaga* **42**, 467-470.

McFadyen, R.E. & Weggler-Beaton, K. (2000) The biology and host specificity of *Liothrips* sp. (Thysanoptera: Phlaeothripidae), an agent rejected for biocontrol of annual ragweed. *Biological Control* **19**, 105-111.

Shea, K. & Kelly, D. (1998) Estimating biocontrol gent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* **8**, 824-32.

Withers, T., McFadyen, R., & Marohasy, J. (2000) Importation protocols and risk assessment of weed biological control agents in Australia: the example of *Carmenta nr. ithacae*. In *Nontarget Effects of Biological Control* (eds P.A. Follett & J.J. Duan), pp. 195-214, Kluwer, Boston.

Prioritising agents based on predicted efficacy: Beyond the lottery approach

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Summary

Concerns over the past 20 years of the increasing environmental risks and economic costs of biological control have led to both external pressures and a desire amongst many biological control practitioners to improve the science behind agent selection. Scientists agree that improving selection of effective agents prior to release is a key to minimising the number of agents necessary for successful control and maximising project success rate. Which agent to import is also costly if misjudged. Divergent opinion remains, however, on whether effective agents can be selected prior to release, because predicting agent performance in new environments is difficult. While critical to success, agent selection remains therefore, one of the least science-based activities in biological control. This paper reviews this debate, ecological theory and the experimental tools available for assessing agent efficacy. These generally focus on the population dynamics of the weed in its target range and estimating the necessary damage types and levels required by agents to reduce weed densities. Weed biological control practitioners are increasingly basing agent selection on likely agent efficacy using these research tools. The only scientific approach to trying to improve agent selection can be the application of such methods, where possible. Explicit decisions made can then be appraised, based on agent performance following release.

Key words: Biological control of weeds, agent selection, population dynamics, agent performance, ecological modelling, impact assessment.

Introduction

Biological control of weeds has been successfully practised in some form for over 200 years (Julien & Griffiths, 1998). Early concerns of collateral damage to plants of economic importance led to a focus on agent specificity as the first key criterion for introduction. The choice of which agent to release was traditionally left to the applied entomologist running the project, but the basis of such selections was rarely documented. It is clearly in the interest of the scientist to select an agent of high efficacy, but other considerations such as ease of rearing and transportation or aesthetics undoubtedly influence such decisions. With the rise of population ecology particularly with respect to natural enemy-plant interactions over the past 30 years, ecological theory and experimental tools for assessing agent efficacy prior to release have become available (Waage, 1991).

Agent efficacy refers to the capacity of an agent population to suppress their host population, more effective agents being those that more quickly suppress their hosts either by attaining very high damage levels or by attacking host stages where relatively small amounts of damage lead to relatively large changes in the dynamics of the host.

Biological control practitioners this century also have a much stronger grounding in ecological principles than their forebears. The value of ecological tools for selecting agents based on likely efficacy and for understanding what makes an effective agent continues, however, to attract vigorous debate (Cullen, 1995; McFadyen, 1998).

Public and political concerns regarding the impacts of biological control on native species and the natural environment through the use of introduced exotic organisms have also been increasing. In the 1980s environmental protection legislation for native species led to much stricter levels of required specificity for biocontrol agents. This change in the perception of risks of biological control, associated with a rising global concern about the effects of exotic species on the environment, has led to critical appraisals of past practice in biological control (when lower levels of agent specificity were acceptable), and pressures to minimise the number of biological control agents used (Simberloff & Stiling, 1996). The low apparent success rate of weed biological control introductions (Julien, 1989) also appears to reflect a poor general capacity to predict which agents will be most effective (Myers, 1985).

Such pressures require biological control practitioners to regularly reappraise the science on which the order of agent introduction is judged to both minimise the total number of agents necessary and to maximize the likelihood of effective weed biological control.

There is general agreement that the biggest challenge to increasing biological control success is improving agent selection (Harris, 1973; Wapshere, 1974; Goeden, 1983; Myers, 1985, 2000; Schroeder & Goeden, 1986; Cullen, 1995; McEvoy & Coombs, 1999; Forno & Julien, 2000), and yet still no widely accepted scientific approach is available. McFadyen (1998), in stating that "agent selection is the critical step, and the choice of the best agent is the 'holy grail' of weed biocontrol", referred not only to the desire of practitioners to make the right choice, but also to the likely impracticality of developing a perfect selection system. Nonetheless, Cullen (1995) argued "if expenditure of public funds is to be justified, if calculated risks have to be taken in introductions, and if we are to manage the science properly to obtain the maximum benefit, we have to try and predict whether an agent will be effective".

Agent selection is really more a process of agent prioritisation (Harris, 1991) than simply trying to pick winners and reject losers (McFadyen, 1998). The list of potential biological control agents drawn up, hopefully following completion of surveys, needs to be prioritised to ensure the agents most likely to be effective are introduced first. If a specific agent fails to be released it is either because it was unnecessary (the project was successful without it) or because project resources ran out. Unfortunately, funding bodies also have a tendency to require quick results and so act as another unhelpful external pressure on how agents are prioritised.

In this paper I present the debate on the relevance of using ecological principles to select and prioritise agents for release based on efficacy. I then review current methods available for assessing likely agent efficacy prior to release. Finally, I argue that the only adaptive or strategic approach to improving agent selection is to apply such methods, where possible, stating clearly the reasoning behind any selections made and assessing any predictions concerning impact following release.

The debate

Myers (1985) first introduced the term "lottery model" to describe where weed biological control is usually achieved by only one of the suite of introduced agents, implying that finding this agent is a lottery. This contrasts with the cumulative stress model where a suite of agents is selected to attack the target in a number of different ways leading to overall suppression. Harris (1991) interpreted the lottery model as equating to sequentially releasing specialised agents until chance alone leads to the one agent that will provide control. In doing so he characterised a philosophical divide amongst biological control practitioners.

One school of thought is that agent efficacy on the target weed following release results from complex interactions between agent and the weed and the new environment (Myers, 1985), and that therefore, predictions of efficacy of biological control agents following release into new environments are not reliable enough to be useful (McFadyen, this proceedings). Weed risk assessment - evaluating plant species for future weediness prior to introduction - is similarly criticised (Groves *et al*., 2001). Host specificity, therefore, remains the only prerequisite for biological control agent selection. This has become known as the lottery approach (*sensu* Harris, 1991) and receives most sympathy within tropical weed systems, where the suite of possible agents is relatively large and the choice therefore particularly difficult. Despite this, it may be hard to imagine such practitioners not applying their intuition or rules of thumb related to likely efficacy when prioritising agents, but they will invest few resources in making this process science-based.

The alternative school argues that the application of ecological studies of both the agent (Edwards *et al.*, 1996; Gassmann, 1996) and the weed (Sheppard *et al.*, 1990; Briese, 1993) enables prioritisation of agents based on likely efficacy. Furthermore, the application of a scientific process to agent selection also allows adoption of the "holistic approach" where the best long-term suppression may come from a community of natural enemies (Waage, 1991). In this case an explicit release strategy can be developed for the sequential release of a combination of compatible agents, while recognising that some agents may interfere with each other or make subsequent agent establishment and the complementary impact of all agents more difficult. This approach tends to have developed through projects that have had good opportunities to carry out ecological studies within the native range of the weed and its natural enemies (Wapshere, 1974). An example of extreme confidence in this system is the view of some scientists in South Africa that new exotic plantation species can now be imported with suites of biological control agents being released concurrently to prevent these exotic plants ever becoming weeds.

These two schools of thought probably represent extremes, and most biological control practitioners' views probably lie along a continuum between them based on their level of confidence in the value of ecological theory and practice for biological control agent selection.

Scientists who have confidence in some capacity for selecting effective agents have sought generalisations to aid agent prioritisation and to develop ecological understanding of effectiveness in biological control agents. Several screening or scoring systems have been proposed to help agent prioritisation, attributing ratings to agents based on biological traits of the weed and the candidate agents (Harris, 1973; Goeden, 1983) or emphasising climatic similarities linked to agent capacities to suppress weed populations in the native range (Wapshere, 1985). These systems required simplicity to minimise data collection requirements and analysis. The weightings used are fairly arbitrary, and the scores are simply summed thereby assuming the relationships between different factors are linear. Recent evaluations suggest that these systems do not provide sufficient resolution to be useful or else invoke false assumptions, i.e. that key factors in a weed's population dynamics are transferable between native and exotic ranges (Böttcher & Lonsdale, 2000). These scoring systems have rarely been employed by others. One exception was Forno & Julien (2000), who applied and adapted these scoring systems to biological control agents used against aquatic weeds in a retrospective analysis and found that the agents that proved to be the most effective also obtained the highest scores.

The "Silwood Project" (Moran, 1986) constructed, via questionnaires, a database on the ecological attributes associated with biological control projects listed in Julien (1987). The resulting analyses by Crawley (1986, 1987, 1989), found successful biological control agents appeared to have correlated taxonomic and biological attributes such as high rates of population increase and multiple generations per year. Certain groups; cochineal insects, weevils, leaf beetles, gall flies, pyralid moths, rusts, etc. or feeding guilds; sap suckers, gall formers, meristem feeders and seed feeders had a better track record. Selecting effective biological control agents, however, is hindered by a plethora of exceptions to such generalities. Crawley (1989) concluded that "biological attributes associated with success have yet to be understood".

This did not prevent intuitive lists of characteristics of agents that should be given high priority being published along with various rules of thumb. Harris (1991), for example, considered high priority agents as being those that; a) have been successful elsewhere, b) have wide geographic ranges, c) have high native parasitism rates, d) attack early in the weed's lifecycle and/or e) are endophagous (can avoid predation). He also considered competitively inferior (k-selected) agents should be released first, to avoid highly competitive (r-selected) agents preventing their establishment or spread. For different weed life history strategies, he argued in favour of root feeders for competitive and clonal plants, defoliators for stress-tolerant plants and any agent that reduces fecundity for annual weeds, maintaining that plants with intermediary life strategies may require additive complementary agents.

Cullen (1995) argued that, despite the existence of many exceptions, suggesting unreliability of lists of generalised characteristics of effective agents, each project can adopt "a questioning approach". This approach might be built around understanding three factors that will dictate the ultimate success of an agent; a) the per capita destructive capacity of the agent, b) ecological and environmental factors likely to determine final agent densities and c) the levels of damage required to suppress the population of the weed. This approach effectively advocates the collection of the types of data that are also necessary for describing the dynamics of agent-weed population interactions. Ecological models built along these lines are now increasingly being used to help understand the ecological processes that will most effectively suppress weed populations. Of Cullen's three categories, however, information on ecological and environmental factors likely to determine final agent densities will always be the hardest to obtain and use to accurately predict agent efficacy.

Ecological and molecular techniques for assessing agent efficacy

Introduced range studies

Studying the ecology and population dynamics of the weeds in the target country, to estimate the key population parameters and life stage transitions is the first step to understanding which factors are most likely to suppress weed populations. These studies are recognised as providing a scientific basis for developing integrated weed management strategies that include all types of weed management. They also provide the baseline data against which the impacts of biological control agents or other weed management strategies can be evaluated. Despite this general recognition, such studies are notoriously under-funded and, where well funded, as for *Mimosa pigra* in northern Australia, are still rarely considered as part of the agent selection process (Forno, 1992).

Smith *et al.* (1993) modelled the population dynamics of the parasitic weed, *Striga hermonthica*, to assess the potential of a weevil as a biological control agent. Understanding of the population dynamics of the weed, however, is not widely accepted as assisting agent prioritisation. Why is this? In most cases the population dynamics indicate that most weed populations experience strongest intraspecific competition at the seedling or juvenile stage, and ecological theory predicts that pest populations are most sensitive to suppression when the damage from weed control options, such as biological control, occurs after such strong density dependence factors operate within the pest population (Waage, 1991). This leads to the unsurprising and intuitively obvious prediction that the most effective weed biocontrol agents (and other weed management strategies) are likely to be those that reduce survival or kill adult plants because such agents would, for a given amount of damage, have a relatively high capacity to suppress target populations. If this is true, then why invest significant resources in studying the population dynamics of each weed? Simple logic has led to strategies that failed to suppress weed populations. For example, encouraged by the successful control of nodding thistle in North America using the flower-head weevil *Rhinocyllus conicus*, subsequent projects on monocarpic weeds adopted a parallel strategy of agents that directly reduced seed production. The argument was simple. The best way to reduce infestations of short-lived weeds reproducing by seed was to try and minimise seed production (R Sohbian, pers. comm.). Suites of seed feeding biocontrol agents were then subsequently released in North America and Australia against each of a number of thistles, knapweeds and legumes. The strategy failed because of a poor understanding of the population dynamics (Powell, 1990; Müller-Scharer & Schroeder, 1993; Kriticos *et al.*, 1999). *Rhinocyllus conicus* was also far less effective against nodding thistle elsewhere it was tried (Woodburn & Cullen, 1993; Kelly & McCallum, 1995). As a result, the use of seed feeders now frequently attracts vigorous debate (Paynter *et al*., 1996; Myers, 2000), despite their continued success as agents against other weeds (Julien & Griffiths, 1998) and as a tool for limiting weed spread.

In contrast, an understanding of weed population dynamics has led to successful strategies targeting the roots and shoots of herbaceous weeds (Blossey *et al.* 1996; Grigulis *et al.*, 2001; Briese & Zapater 2002; Briese *et al.* 2002) or using complementary agents against a woody weed (Hoffmann, 1990). What constitutes the most effective agent, therefore, relates to some degree to the detailed population dynamics of the target and the potential agents available. Ecological generalisations are apparently not enough to maximise the success of all biological control projects.

Experiments using artificial reductions of weed or seed density in the target country can help assess the necessary damage thresholds required to suppress weed populations or can determine vulnerable points in the life cycle (Harris, 1991). However, these are rarely carried out (e.g. Smyth *et al.*, 1997). Perhaps the results end up being too site specific and are therefore not considered worth the cost. One solution may be to incorporate weed reduction treatments within trials of integrated weed management strategies (Huwer *et al.*, 2002). More frequently, such manipulations are made as sensitivity analyses of growth survival and fecundity parameters in ecological models built from demographic studies (Rees & Paynter, 1997; Kriticos *et al.*, 1999; Sheppard *et al.*, 2002a, 2002b, Buckley *et al.*, in press). This approach represents the increasing use of prospective modelling as a tool to predict vulnerable points in the life cycle of the weed and the dynamical outcome of introducing agents as a method of agent selection (Waage, 1991). Either way such manipulations can suggest the types of agents required. Seed addition experiments can detect seed limitation in weed populations and are considered by some as highly advisable before deciding on a strategy employing seed feeding agents (Myers, 2000).

Field surveys

Adopting quantitative over qualitative agent survey methods in the native range may assist agent prioritisation. Quantitative surveys provide relative abundances of the different potential agents and can estimate variation in field attack levels (Sheppard *et al.*, 1994, 1995; Briese, 2000). Survey data can be collected in manner that allows estimation of, for example, the impact of agents, such as seed feeders on seed production per plant (Briese, 2000). Most published quantitative surveys, however, only provide data on agent attack rates. Agents that at least occasionally outbreak in the native range may be under some suppressive effect from low host plant abundance or high native parasitism, while potential agents that are always rare may remain so even in the new environment. Furthermore, ecological theory predicts that agents more abundant in low density host populations may be those best adapted to maintain weeds at native range levels (Waage, 1991). As indicated by many authors, wide geographic range (Harris, 1991) and high levels of native parasitism (Gassmann, 1996) suggest a capacity for rapid increase in density and range expansion following release.

Other native range studies

Contrary to early arguments (Wapshere, 1974, 1985), studying the population dynamics of the target weed in its native range less frequently provides direct help to agent prioritisation. Native populations are usually small and scattered (Schroeder & Goeden, 1986), and few are being suppressed by natural enemies (Sheppard *et al.*, 1991; Sheppard, 1996; Paynter *et al.*, 1998). The big successes in biological weed control show that with a super abundance of their hosts and/or in the absence of their native natural enemies, agents can still limit their host populations in the exotic range. Where weeds are almost as common in their native range as where introduced, biological control depends on agents that are being limited by their natural enemies in the native range (rather than bottom up regulation via plant resources) (Straw & Sheppard, 1995).

In contrast, if a potential agent can be shown to suppress the dynamics of its host in the native range, or is even just capable of killing its host, then this is a very positive sign of likely efficacy (Myers, 2000). Such agents may be capable of suppressing the target at relatively low host densities and in the presence of their native predators. Sheppard *et al.* (1994) found seed predation levels in native populations of *Carduus nutans* were between 81 to 99% leading to seed limitation in these native thistle populations. The dominant seed predator was the weevil, *Rhinocyllus conicus*, supporting its efficacy against this thistle in North America (cf. Woodburn & Cullen, 1993), albeit also an effective threat to native thistles (Louda & Arnett, 2000).

Native range studies of weed population dynamics when compared to, or better still when conducted in parallel with similar studies in the exotic range can suggest the main reasons why these plant species have become invaders. These indicate the parts of the weeds life cycle that have undergone ecological release following introduction (Sheppard, 2000; Grigulis *et al.*, 2001). Such studies have shown that this generally occurs through higher production of propagules in the invaded environment (Noble, 1989).

Impact experiments conducted in the native range are the other main technique for assessing agent efficacy and might be conducted as extensions of field tests of host specificity. These involve manipulating densities of the agents on experimental plants preferably in natural field conditions (Hasan & Aracil, 1991; Brun *et al.*, 1995) or with cages (e.g. Müller-Schärer, 1991) and measuring changes in weed growth, survival and reproduction. The cages help separate the impacts of the different species of natural enemy and other factors such as interspecific competition (Sheppard, 1996). Such experimental studies can also provide measures of per capita impacts of potential biological control agents (e.g. Sheppard *et al.*, 1994). These and information on the natural local agent distribution pattern can allow agent densities to be related to required damage levels for weed suppression estimated from the target range studies. This may be assisted by agents achieving densities orders of magnitude higher, following release, than found in the native range (Sheppard *et al.*, 2002b). Briese (1996a) used such cage studies to predict likely impacts of resident densities of the stem boring weevil *Lixus cardui* on seed production of its *Onopordum* thistle hosts following release in Australia. The observed densities of the weevil following release exceeded expectations causing high seed losses in a manner that complements the activities of other agents (A. Swirepik, pers. comm.).

Native trap gardens of high weed density can similarly be constructed, into which agents can be released. Where agents are normally limited by bottom up processes like weed density in the native range, their populations may increase in the trap gardens; a sign of what may happen after release. All the potential agent species might be released concurrently into the trap gardens, speeding up the assessment process and, when test plants are included, such gardens provide an additional role in field host range testing.

Techniques for selecting pathogens

Plant pathologists are involved in agent selection even after the decision to release a particular species of pathogen has been taken. The existence of many strains within species of plant pathogens such as rust fungi, necessitates selecting the most effective. As with arthropod biological control agents, final efficacy will depend on the interaction between any given pathogen strain and the new environment. While laboratory testing of relative pathogenicity (ability to cause disease on target genotypes) and aggressiveness (amount of damage caused) are frequently used in such cases, the results are not highly reliable predictors of what will happen in the field following release. Matching the climate between the collection area and the release area may be as reliable an approach. The discovery of the correct strain of *Puccinia chondrillina* when released against the dominant clone of skeleton weed in Australia in the 1970's, came about more through luck than a science-based approach (S. Hasan pers. comm.), although field studies had shown that this pathogen was generally important in the population dynamics of its host in the native range (Waphsere 1985). In a study of the leaf blight fungus, *Cercospora heliotropii-bocconii*, for release against the toxic annual weed *Heliotropium europaeum*, the question was, would this exotic species be more damaging than a closely related species, *Cercospora taurica*, already causing epidemics against the target in Australia? Comparative field (Brun *et al.* 1995) and laboratory studies using various strains of the pathogen (L. Brun and L. Morin unpublished data) could not conclusively affirm this and so introduction was not pursued. Efficacy of another pathogen, *Uromyces heliotropii*, against this target was also tested in the field in the native range under experimental conditions for perhaps the first time using a pathogen (Hasan & Aracil 1991). This study failed to recognise, however, that the weak link in the efficacy of this agent was the sexual cycle in early spring, which provided an annual bottleneck to disease persistence and spread following release. This problem might have been anticipated from the infrequency of this pathogen in regions of similar climate to Australia (A. Sheppard personal observation).

The increasing importance on plant pathogens in the armoury of potential biological control agents has and will increasingly lead to the need to choose between a range of available potential pathogens or indeed between a pathogen or an arthropod agent. In the former case, rules of thumb are still generally used.

Species that in addition to infecting a single host a) cause significant damage b) have a simple lifecycle c) can persist without sexual reproduction and c) can occur frequently and abundantly in matching climates to the target range are worth noting. Selecting between a pathogen or an arthropod agent has received little discourse in the literature, but, as someone who has worked with both, my intuition suggests, if the pathogen has all the right characteristics, try it first, even more so if the target is either an ephemeral or a large woody weed. In the latter case a systemic fungus would be even better. Also pathogen and arthropod agents are usually quite compatible when released together, as has been observed with the leafhopper and rust on bridal creeper (L. Morin, unpublished).

Molecular studies

Molecular techniques are revolutionising biological control (IOBC, 2002). Their primary role is in target agent identification and characterising their population structures and phylogenetic relationships. While this does not predict agent efficacy, by providing resolution at the sub-specific level of the target or agent clade and between-population structure, precise matching to hosts and climate in both the native and exotic range can be assured (Briese, 1996b). This has been particularly true for plant pathogens where there can extremely tight specificity relationships between strains of pathogen and target. Opportunities for restarting the biological control of certain blackberry clones using the corresponding strains of the rust *Phragmidium violaceum* have been made possible through application of molecular techniques (Evans *et al.* 1998, 2000). Characterisation of mechanisms for incorporation and persistence of new genes, such as those conferring virulence, into an existing pathogen population, may also provide a theoretical basis for agent selection and release (Evans & Gomez, in press).

Using DNA studies, Fumanal et al. (2002) found that only one of four separate morphologically indistinguishable clades of the stenophagous weevil *Ceutorhynchus assimilis* that forms large collar galls on the cruciferous weed *Cardaria draba* is highly specific, opening a door for it as a biological control agent. Also the failure to select effective agents against *Lantana* spp. in Australia may have resulted from a poor understanding of the taxonomy of the genus now being revealed using DNA studies (Scott *et al*., 2002). Such studies can also provide the precise range of origin of the target and the target centre of diversity. Information on weed reproductive systems, such as degree of outcrossing (Michalakis *et al*., 1993a) or clonal structure, can also be obtained. Similarly, knowing geographic patterns in agent population structure provides evidence of likely agent dispersal distances prior to release (Michalakis *et al*., 1993b).

Parallels with weed risk assessment

As previously mentioned, there are parallels between the process in weed risk assessment of trying to select which plant species, proposed for introduction into a new region, will become future weeds, and trying to select which agent, from a suite of potential biological control agents, will be the most effective. Both processes involve the selection of a biological organism based on its capacity to invade and reach high population density. Also both processes require that the decision is made based on a range of available biological characteristics, but with poor information on how well the organism will perform in the conditions found in the new environment. Finally, both processes rely, in part, on how the organism has performed in other similar climates. Weed risk assessment has its critics (Smith *et al.*, 1999) as decision theory shows that it is hard to pick which species will be an important invasive weed when the proportion of introduced species likely to become such is extremely low (ca. 1 per 1000 for plants). This proportion is called the base rate. The key difference between weed risk assessment and biological control agent selection is the size of this base rate, as roughly 1 in 5 agents released for the biological control of weeds has been involved in successful weed control (Julien, 1989). The chance of making the right informed decision in biocontrol agent selection is therefore roughly 200 times greater than in weed risk assessment. Nonetheless weed risk assessment attracts increasing interest and adoption (Groves *et al.*, 2001), while the value of science-based selection of effective agents is still a subject of debate.

A strategic approach

Biological control practitioners are part of a small privileged group of scientists with permission to release new species into the environment for the benefit of agriculture and biodiversity and study what happens. With this responsibility comes accountability. The number and nature of such releases will increasingly require justification. A selection process based on chance alone appears hard to justify, not least because it provides no opportunity to improve or refine the process. Waage (1991) argues that it is better to make some form of judgement based on accepted ecological principles than to flip a coin. At least the value of the judgement can be assessed in the future. While universal criteria for agent selection still appear unlikely, documenting a process of assessment tailored to each project may, over many projects, provide some more reliable rules of thumb. Increasing needs to assess risks to non-targets (Willis *et al.*, these proceedings) may also benefit from focused ecological research on likely agent efficacy (Louda, 2000).

Improving the science behind agent selection will require being able to retrospectively assess the success of agent release strategies, project by project. Such strategies therefore need to be declared from the outset, including, not only which agents will be released and in what order, but also why agents are to be released in that order. This is rarely done (e.g. Blossey *et al.*, 1996; Briese & Zapater, 2002; Briese *et al.*, 2002). This should allow strategies across targets of similar and contrasting life history strategies to be compared and improved.

Even if there is some degree of acceptance that ecological studies can assist agent selection, the level to which such studies can be carried out will be largely determined by available resources. Whether each activity is worth the resource cost will depend on the importance of the weed and the complexity of the selection process, i.e. the number of agents to choose from. If recent analyses are correct and successful biological control is usually achieved by one rather than multiple agents (Forno & Julien, 2000; Denoth *et al*., 2002), then the higher the number of potential agents e.g. in many (tropical) woody weeds the greater the investment should be in the decision process. In this regard it might be of value to retrospectively analyse decisions taken in the biological control program against *Lantana camara*. This is the largest and longest running and so far least successful (with respect to investment) biological control of weeds program in Australia and probably the world. Twenty nine agent species have been released in Australia and 36 species worldwide (Julien & Griffiths, 1998). Why was it that each agent was released? For each new agent, why was this released in addition to those already present? Valuable lessons may be learned, and this project is one in which agent selection has room to improve in the future.

A range of project characteristics will influence the level of investment made in ecological studies of agent efficacy. These might include a) the potential benefit from success, b) the number of potential agents available, c) the risk to non-targets, d) the project budget, d) perceived urgency, or e) previous success in that system. There appear to be sufficient ecological tools available now to allow weed biological control to move away from the early 20th century applied entomologist making a simple experience-based value judgement on agent prioritisation. Release strategies, if clearly declared, can be assessed and reviewed by others. Such research activities mean that potentially the most costly decision made by biological control practitioners may no longer need to be left to chance.

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References

Blossey, B., Malecki, R.A., Schroeder, D. & Skinner (1996) A biological weed control program using insects against purple loosestrife (*Lythrum salicaria*) in North America. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 351-356. University of Cape Town, South Africa.

Böttcher, S. & Lonsdale W.M. (2000) Evaluating the efficiency of agent prioritisation tools. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 592, Montana State University, Bozeman.

Briese, D.T. (1993) The contribution of plant biology and ecology to the biological control of weeds. *Proceedings of thee 10th Australian & 14th Asian-Pacific Weed Conference*, pp. 10-18, Weed Society of Queensland, Brisbane.

Briese, D.T. (1996a) Potential impact of the stem-boring weevil *Lixus cardui* on the growth and reproductive capacity of *Onopordum* spp. thistles. *Biocontrol Science and Technology* **6**, 251-261

Briese, D.T. (1996b) Phylogeny: can it help us to understand host choice by biological weed control agents? *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 63-70. University of Cape Town, South Africa.

Briese, D.T. (2000) Impact of the *Onopordum* capitulum weevil *Larinus latus* on the reproductive potential of its host plant. *Journal of Applied Ecology* **37**, 238-246.

Briese, D.T. & Zapater, M. (2002) A strategy for the biological control of blue heliotrope *(Heliotropium amplexicaule). Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 394-397, Plant Protection Society of WA Inc, Perth.

Briese, D.T., Petit, W. Swirepik, A. & Walker A. (2002) A strategy for the biological control of *Onopordum* spp. Thistles in south-eastern Australia. *Biocontrol Science and Technology* **12**, 121-137.

Brun, L.A., Sheppard, A.W., Delmotte, E., Hasan, S., Jourdan, M. (1995) Development of cercospora blight epidemics and effect on the summer annual *Heliotropium europaeum* in the field. *Annals of Applied Biology* **127**, 137-150.

Buckley, Y. M., Briese, D. T. & Rees, M. (2003). Demography and management of the invasive plant species *Hypericum perforatum*: 2. Construction and use of an individual-based model to predict invasion dynamics and the effects of management strategies. *Journal of Applied Ecology* **40**, in press.

Crawley, M.J. (1986) The population biology of invaders. *Philosophical Transactions of the Royal Society of London B* **314**, 711-731.

Crawley, M.J. (1987) What makes a community invasible? *Colonisation Succession and Stability* (eds A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 429-454, Blackwell, Oxford.

Crawley, M.J. (1989) The successes and failures of weed biocontrol using insects. *Biological Control News and Information* **10**, 213-223.

Cullen, J. M. (1995) Predicting effectiveness: Fact and fantasy. *Proceedings of the VIII International Symposium on Biological Control of Weeds* (eds. E.S. Delfosse & R.R. Scott), pp. 103-110. CSIRO Publishing, Melbourne.

Denoth, M., Frid, L. & Myers J.H. (2002) Multiple agents in biological control: improving the odds? *Biological Control* **24**, 20-30.

Edwards, P.B., Adair, R.J. & Holtkamp, R.H. (1996) Seedhead tephritids and their parasitoids- can predictions be made about likely parasitism of tephritids introduced into Australia for biological control of Asteraceae? *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 153-164. University of Cape Town, South Africa.

Evans, K.J., Symon, D.E. & Roush, R.T. (1998) Taxonomy and genotypes of the *Rubus fruticosus* L. aggregate in Australia. *Plant Protection Quarterly* **13**, 152-156.

Evans, K.J., Jones, M.K., Mahr, F.A. & Roush, R.T. (2000) DNA phenotypes of the blackberry biological control agent, *Phragmidium violaceum,* in Australia. *Australasian Plant Pathology* **29**, 249-254.

Evans, K.J. & Gomez D.R. (in press) Weed management using introduced rust fungi and population genetic questions. In *The Role of Genetics and Evolution in Biological Control*, CABI Publishing, Wallingford.

Forno, I.W. (1992) Biological control of *Mimosa pigra*: Research undertaken and prospects for effective control. *A Guide to the management of* Mimosa pigra. (ed. K. Harley), pp. 38-42, CSIRO Canberra.

Forno, I.W. & Julien M.H. (2000) Success in biological control of aquatic weeds by arthropods. *Biological Control: Measures of Success* (eds G Gurr & S Wratten), pp. 159-188, Kluwer Academic Publishers, Dordrecht.

Fumanal, B., Martin, J.-F., Sobhian, R., Lumeret, J.-P. & Bon, M.-C. (2002) Host-associated differentiation of the collar gall weevil *Ceutorhynchus assimilis* (Coleoptera: Curculionidae) and insights in biological control. In *The Role of Genetics and Evolution in Biological Control, (Abstract volume)*. Global IOBC, Montpellier, France.

Gassmann, A. (1996) Classical biological control of weeds with insects: a case for emphasizing agent demography. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 171-176. University of Cape Town, South Africa.

Goeden, R.D. (1983) Critique and revision of Harris' scoring system for selection of insect agents in biocontrol of weeds. *Protection Ecology* **5**, 287-301.

Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves RH (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges *Journal of Applied Ecology* **38**, 281-290.

Groves, R.H., Panetta, F.D. & Virtue, J.G. (2001) *Weed Risk Assessment*, CSIRO Publishing Melbourne.

Harris, P. (1973) The selection of effective agents for the biological control of weeds. *Canadian Entomologist* **105**, 1495-1503.

Harris, P. (1991) Classical biocontrol of weeds: Its definition, selection of effective agents, and administrative – political problems. *Canadian Entomologist* **123**, 827-849.

Hasan, S. & Aracil, E. (1991) Biology and effectiveness of *Uromyces heliotropii*, a potential biological control agent for *Heliotropium europaeum. New Phytologist* **118**, 559-563.Smith, C.S., Lonsdale, W.M. & Fortune, J. (1999) When to ignore advice: invasion predictions and decision theory. *Biological Invasions* **1**, 89-96.

Hoffmann, J.H. (1990) Interactions between three weevil species in the biocontrol of *Sesbania punicea* (Fabaceae): the role of simulation models in evaluation. *Agriculture, Ecosystem and Environment* **32**, 77-87.

Huwer, R.K., Neave, M.J., Dowling, P.M., Lonsdale, W.M., Sheppard, A.W., Briese, D.T. & Michalk, D.L. (2002) Integrated weed management (IWM) in perennial pasture using pasture and grazing management, herbicide strategies and biological control. *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 727-730, Plant Protection Society of WA Inc, Perth.

IOBC (2002) *The Role of Genetics and Evolution in Biological Control (Abstract volume)*. Global IOBC, Montpellier, France.

Julien M.H. (1987) *Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds (2nd Edition)*. CAB, Wallingford

Julien, M.H. (1989) Biological control of weeds worldwide: trends, rates of success and the future. *Biological Control News and Information* **10**, 299-306.

Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds (4th Edition)*. CABI, Wallingford.

Kelly, D. & McCallum, K. (1995). Evaluating the impact of *Rhinocyllus conicus* on *Carduus nutans* in New Zealand. *Proceedings of the VIIIth International Symposium on Biological Control of Weeds* (ed E.S. Delfosse & R.R. Scott). pp 205-212, CSIRO Publications, Melbourne

Kriticos, D.J., Brown, J.R., Radford, I.D. & Nicholas, M. (1999) Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control* **16**, 230-9.

Louda, S.M. (2000) *Rhinocyllus conicus* – insights to improve predictability and minimize risk of biological control of weeds. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 187-193. Montana State University, Bozeman.

Louda, S.M. & Arnett, A.E. (2000) Predicting non-target effects of biological control agents: evidence from *Rhinocyllus conicus*. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed.N.R. Spencer), pp. 551-567. Montana State University, Bozeman.

McFadyen, R.E.C. (1998) Biological control of weeds. *Annual Review of Entomology* **43**, 369-393.

McEvoy, P.B. & Coombs, E.M. (1999) Biological control of plant invaders: Regional patterns, field experiments, and structured population models. *Ecological Applications* **9**, 387-401.

Michalakis, Y., Derancourt, F., Noël, V. & Espiau, C. (1993a) A first estimation of the mating system of *Onopordum illyricum* (L.) and its relevance to the invasion of Australia. *Acta Oecologica* **14**, 539-545.

Michalakis, Y., Sheppard, A.W., Noël, V. & Olivieri, I. (1993b) Population structure of a herbivorous insect and its host plant on a microgeographic scale. *Evolution* **47**, 1611-1616.

Moran, V.C. (1986) The Silwood International Project on the biological control of weeds. *Proceedings of the VI International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 65-68. Agriculture Canada, Vancouver.

Müller-Schärer, H. (1991) The impact of root herbivory as a function of plant density and competition: survival, growth and fecundity of Centaurea maculosa in field plots. *Journal of Applied Ecology* **28**, 759-776.

Müller-Schärer, H. & Schroeder, D. (1993). The biological control of *Centaurea* spp. in North America: Do insects solve the problem? *Pesticide Science* **37**, 343-353.

Myers, J.H. (1985) How many insect species are necessary for successful biocontrol of weeds? *Proceedings of the VI International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 77-82. Agriculture Canada, Vancouver.

Myers, J.H. (2000) What can we learn from biological control failures? *Proceedings of the X International Symposium on Biological Control of Weeds* (ed.N.R. Spencer), pp. 151-154. Montana State University, Bozeman.

Noble, I. R. (1989) Attributes of invaders and the invading process: Terrestrial and vascular plants. *Biological Invasions: a Global Perspective* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Burger, M. Rejmanek & M. Williamson), pp. 301-310. J. Wiley & Sons, Chichester.

Paynter, Q., Fowler, S.V., Hinz, H.L., Memmott, J., Shaw, R., Sheppard, A.W. & Syrett, P. (1996) Are seed-feeding insects of use for the biological control of broom? *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 495-502. University of Cape Town, South Africa.

Paynter, Q., Fowler, S. V., Memmott, J. & Sheppard A.W. (1998) Factors affecting the establishment of *Cytisus scoparius* in southern France: implications for its control. *Journal of Applied Ecology* **35**, 582-595.

Powell, R.D. (1990) The functional forms of density-dependent birth and death rates of diffuse knapweed (*Centaurea diffusa*) explain why it has not been controlled by *Urophora affinis, U. quadrifasciata* and *Sphenoptera jugoslavica*. *Proceedings of the VIIth International Symposium on Biological Control of Weeds* (ed E.S. Delfosse) pp. 195-202. Instituto Sperimentale per la Patologia Vegetale, Rome, Italy

Rees, M. & Paynter, Q. (1997) Biological Control of Scotch Broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology* **34**, 1203-1222.

Schroeder, D. & Goeden, R.D. (1986) The search for arthropod natural enemies of introduced weeds for biological control – in theory and practice. *Biological Control News and Information* **7**, 147-155.

Scott, L.J., Hannan-Jones, M.A. & Graham, G.C. (2002) Affinities of *Lantana camara* in the Australia-Pacific region. *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 471-474, Plant Protection Society of WA Inc, Perth.

Sheppard, A.W. (1996) The interaction between natural enemies and interspecific plant competition in the control of pasture weeds. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran & J.H. Hoffmann), pp. 47-54. University of Cape Town, South Africa.

Sheppard, A.W. (2000) Weed ecology and population dynamics. *Australian Weed Management Systems*. (ed. B. Sindel). pp. 39-60. RG and FJ Richardson Press, Melbourne.

Sheppard, A.W., Cullen, J.M., Aeschlimann, J.P., Sagliocco, J.L. & Vitou, J. (1990) The importance of insect herbivores relative to other limiting factors on weed population dynamics: a case study of *Carduus nutans*. *Proceedings of the VII International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 211-219. MAF, Rome.

Sheppard, A.W., Aeschlimann, J.-P, Sagliocco, J.-L. & Vitou, J. (1991) Natural enemies and population stability of the winter-annual *Carduus pycnocephalus* L. in Mediterranean Europe. *Acta Oecologica* **12**, 707-726.

Sheppard A.W., Cullen J.M., Aeschlimann J-P (1994) Predispersal seed predation on *Carduus nutans* (Asteraceae) in southern Europe. *Acta Oecologica* **15**, 529-541.

Sheppard, A.W., Aeschlimann, J.-P., Sagliocco, J.-L. & Vitou, J. (1995). Below ground herbivory in *Carduus nutans* (Asteraceae) and the potential for biological control. *Biocontrol Science & Technology* **5**, 261-270

Sheppard, A.W., Hodge P., Paynter, Q. & Rees, M. (2002a). Factors affecting invasion and persistence of broom, *Cytisus scoparius*, in Australia. *Journal Applied Ecology* **39**, 721-734.

Sheppard, A.W., Rees, M., Smyth, M., Grigulis, K. & Buckley Y. (2002b) Modelling the population interactions between the crown weevil *Mogulones larvatus* and its host plant *Echium plantagineum*. *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 248-251, Plant Protection Society of WA Inc, Perth.

Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology* **77**, 1965-1974.

Smith, C.S., Lonsdale, W.M. & Fortune, J. (1999) When to ignore advice: invasion predictions and decision theory. *Biological Invasions* **1**, 89-96.

Smith, M.C., Holt, J. & Webb, M. (1993) A population model for the parasitic weed *Striga hermonthica* (Scrophulariaceae) to investigate the potential of *Smicronyx umbrinus* (Coleoptera: Curculionidae) for biological control in Mali. *Crop Protection* **12**, 470-476.

Smyth, M.J., Sheppard, A.W. & Swirepik, A. (1997) The effect of grazing on seed production in *Echium plantagineum* L. *Weed Research* **37**, 63-70.

Straw, N.A. & Sheppard, A.W. (1995) The role of plant dispersion in the success and failure of biological control. *Proceedings of the VIII International Symposium on Biological Control of Weeds* (eds. E.S. Delfosse & R.R. Scott), pp. 161-170. CSIRO Publishing, Melbourne.

Waage, J. (1991) Ecological theory and the selection of biological control agents. *Critical Issues in Biological Control* (ed. A. MacKauer), pp. 135-157, Intercept, Andover.

Wapshere, A.J. (1974) A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology* **77**, 201-211.

Wapshere, A.J. (1985) Effectiveness of biological control agents for weeds: present quandaries. *Agriculture Ecosystems and Environment* **13**, 261-280.

Woodburn T.L. & Cullen J.M. (1993) Effectiveness of *Rhinocyllus conicus* as a biological control agent for nodding thistle, *Carduus nutans*, in Australia. *Proceedings of the 10th Australian & 14th Asian-Pacific Weed Conference*, pp. 99-103, Weed Society of Queensland, Brisbane.

The centrifugal phylogenetic method used to select plants for host-specificity testing of weed biological control agents: Can and should it be modernised?

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Summary

The current model for test plant selection, the centrifugal phylogenetic method, has been used for the past 28 years, during which time there have been considerable advances in knowledge of host-choice evolution and plant phylogeny. This paper re-examines the premises of the centrifugal phylogenetic method and, in light of this, proposes a "modernisation" of the method within a framework of risk assessment. In the case of non-target plant species, several elements contribute to the potential level of risk; phylogenetic relatedness, biogeographic overlap and ecological similarity. Test plants are selected using criteria based on these elements of risk. Plants are categorised according to their degree of phylogenetic separation from the target weed rather than by taxonomic circumscription, as is current practice. Examples are given of this approach, which obliges a closer examination of plants with one to a few degrees of phylogenetic separation and less attention to those more distantly separated plants, enabling a more accurate assessment of actual risk without losing any information on agent host-range. Evidence is also presented that many of the gaps in knowledge of host-plant relationships, for which the use of safeguard species was recommended, are now filled. This, and the fact that their use has not contributed information on agent host affiliations, suggests that their inclusion in test lists is no longer warranted. The proposed "modernisation" is intended as a starting point for debate on the improved selection of test plants. It is recognised that science cannot be divorced from politics in issues that involve government regulation, and any move to change the basis by which we select test plant should be done in collaboration with the regulatory authorities concerned.

Key words: host-specificity testing, plant phylogeny, risk assessment, biological weed control

Introduction

The discipline of weed biological control prides itself in the attention it has historically given to the safety-testing of candidate control agents, in contrast to related biocontrol disciplines targeting insects and vertebrate pests, where the absence of specificity-testing has led to many cases of non-target damage (e.g. Howarth, 1983; Simberloff & Stiling, 1996). The initial driver for testing weed biological control agents was to allay public fear of damage to economically useful plants (see Huffaker, 1957; Wapshere, 1974; Harris, 1998). Such testing was first done during the 1920s in the Australian project against *Opuntia*, where it was the policy of the Commonwealth Prickly Pear Board that no insect would be released until it was proved "safe" through a series of starvation tests (Dodd, 1940). Selection of species for testing was initially not done systematically, but, underpinned by developments in knowledge of host-choice by phytophagous insects, a protocol evolved over the next fifty years (see Harris, 1998). From having the primary aim of determining whether particular crop plants were safe, congeneric and related plants from broader taxa were increasingly included in testing protocols to more systematically determine host-range limits. Harris & Zwölfer (1968) were the first to propose a more "biologically relevant" set of guidelines for the selection of test plants, though the emphasis remained focussed on plants considered useful. Finally, Wapshere (1974) expanded and formalised the rules for selecting test plants under the name of the centrifugal-phylogenetic method (CPM). This remains the standard for host-specificity testing today, and has served biological control practitioners in good stead over the past 28 years. In fact, Wapshere's original paper has been increasingly cited in weed biological control literature in support of the selection of test plants for candidate control agents (80 of the 125 citations listed by ISI Web of Science® have appeared in the last 10 years).
In addition, the CPM is generally accepted by government regulatory authorities.

Since 1974, change has occurred in two directions. Within the discipline, debate has turned more towards the methodology of host-specificity testing, with the aim of producing biologically more realistic tests and more accurate assessments of risk to selected plants (see Withers *et al.*, 1999; van Driesche *et al*., 2000). In addition, there has been a societal paradigm shift towards recognising the value of "non-useful" indigenous plants as part of our biological heritage. This has led to increasing inclusion of such species in test lists, though selected under the same set of rules. Indeed, this shift has put weed biological control and its practices under much stronger scrutiny in cases where native non-target plants were considered to be at risk (Strong, 1997; Louda, 2000). Despite this, apart from greater attention to indigenous flora, there has been no attempt to "modernise" the CPM to address these contemporary issues, although Harris & McEvoy (1995) have called for testing procedures to be expanded to include phylogenetic, bioclimatic and biological constraints.

Given the political acceptance of the CPM, should biological control practitioners be looking to change the way test lists are selected? On the one hand, the status quo is comfortable and acceptable, while on the other hand, continuing advances in our knowledge of the phylogenetic relationships of plants, the host-choice behaviour and evolution of host-choice in phytophagous insects, and the infection processes of pathogens suggest that it is at least time to critically review the premises of the model. This paper examines the rationale behind the CPM and examines the criteria upon which it is based. On this basis, it proposes a different approach to the way in which phylogenetic data is used for the selection of test plants, based primarily on the consideration of risk. It is intended that this model serves as a starting point for further debate on this aspect of the host-specificity testing process in weed biological control.

The centrifugal phylogenetic model – a commentary

As described by Wapshere (1974), the CPM comprises a core component, based on exposing a candidate agent to a sequence of test plants, from those most closely related to the target weed to those belonging to successively more distant taxa (Table 1). This is supported by a safeguard component, used to incorporate additional plants that would not be selected as part of the first component, based on several criteria designed to cover gaps in knowledge of host-plant relationships.

Component A – selection of test plants in order of taxonomic relatedness

This sequential testing pattern was based on knowledge that host-choice is governed by a hierarchical set of behavioural and physiological responses to visual, tactile and chemical cues provided by the various plants that a phytophagous insect might encounter. In the case of pathogens, such responses would be solely physiological as host location is a passive process. For all specialist natural enemies, host usage is mediated by ecological and phenological adaptations that ensure that the life-cycles of the agent and its host-plant are attuned in time and space. The information available at the time CPM was developed is well summarised by Huffaker (1957) and Zwölfer & Harris (1971), and is reinforced by more recent studies (see Bernays, 2000). This means that the more closely related plant species are, the more similar are aspects of their morphology and chemistry, and the more likely they are to possess cues that will be recognised as a host by particular phytophages. Recent evidence on the evolution of insect-plant associations confirms this association (see Mitter *et al.*, 1991; Futuyma, 2000); host-shifts in lineages of specialist phytophagous insects are linked to the evolution of host-plant lineages, in particular to plant chemistry, and there is evidence of a strong phylogenetic conservatism of host associations. The scientific support for this core component of CPM is therefore even stronger today.

Table 1. Testing sequence as recommended by the centrifugal phylogenetic method (after Wapshere, 1974).

Sequence	Plants to be tested
1	Other forms of the same species
2	Other species within the genus
3	Other members of the tribe
4	Other members of the subfamily
5	Other members of the family
6	Other members of the order

There is, however, one flaw to this component of CPM. Briese *et al.* (2002) pointed out that, while it claims to be phylogenetically-based, in practice it is largely based on taxonomic circumscription. This is not necessarily a trivial or pedantic differentiation, as phylogenetic classification by definition reflects the evolutionary history of a group of organisms whereas Linnean taxonomic classification need not. Formal taxonomic rankings (i.e. order, family, subfamily etc) are not always informative of the evolutionary history of organisms; they may be polyphyletic or paraphyletic or, at the species level, may contain several distinct monophyletic lineages that have not been recognised by the genus or species circumscriptions. The latter may be particularly important for insects with very narrow host-associations such as those sought for weed biological control.

Increasingly, modern molecular studies are revealing such "flaws" in the Linnean classification system. A good example of this is the genus *Acacia* (tribe Acacieae), where recent molecular studies have shown that the genus is paraphyletic, with Australian *Acacia* species being more closely related to genera in the related tribe Ingaeae than to African *Acacia* species (Miller & Bayer, 2001). Mishler (1999) has expressed concerns that the non-equivalence of taxonomic ranks may make them, at best, meaningless and, at worst, "can lead to bad science in the hands of a user of classifications who naively assumes that groups of the same rank are comparable" (Mishler, 1999). The clades derived from phylogenetic analyses, on the other hand, are strictly monophyletic, and this can have implications for the structure of plant lists, as will be shown later.

While generally not following a pattern of co-speciation, host-choice of specialist natural enemies is taxonomically conservative and highly associated with plant phylogeny, particularly at lower level clades (below the tribe taxon) (see Mitter *et al*., 1991; Briese, 1996; Fuytuma, 2000). We may therefore be misled by strict reliance on the circumscriptions of a taxonomic ranking system.
An illustration of this is the genus *Heliotropium*, where there are 70 described species endemic to Australia (Craven, 1996). These became primary test plants for a candidate biological control agent of the invasive South American weed, *Heliotropium amplexicaule*. Testing showed that the agent, Deuterocampta quadrijuga (Coleoptera: *Chrysomelidae*) discriminated strongly within the genus level, having a small group of South American *Heliotropium* species as primary hosts, showing some ability to survive on other South American species, but rejecting the Australian species (Briese & Walker, 2002). Molecular studies of the Boraginales conducted independently to this work confirmed that there was a major phylogenetic split between Australian and South American members of the genus (Gottschling *et al*., 2001) and, in fact, Australian species will soon be reassigned to a separate genus, *Euploca* (H. Hilger, pers. comm.). Molecular evidence also showed species of the genus Tournefortia nested within the South American Heliotropium (Gottschling *et al*., 2001), which may explain the apparent anomaly of Tournefortia sarmentosa being more acceptable to *D. quadrijuga* than Australian *Heliotropium* species (Briese & Walker, 2002). Phylogenetic studies therefore confirmed what host-testing had implied about plant relationships and the likelihood of being a host-plant for *D. quadrijuga*. This supports the reverse argument that a test plant list which focuses on actual phylogenetic relationships will more accurately reflect the limits of phytophage host associations than one for which such relationships were not considered. It is further supported by evaluations of biological control releases which indicate that non-target plant species colonised by an agent are either congeneric or from closely related genera (Pemberton, 2000).

While in practice biologically relevant factors, such as plant morphology, biochemistry and distribution, may be used to select representative plants within taxonomic circumscriptions (Forno & Heard, 1997), there is often undue emphasis on testing certain named taxa, leading to misplaced impressions of precision. Briese & Walker (2002) pointed out that, in the Australian peer-reviewed system, proposed test lists have often had additional species suggested on the basis that a particular genus, tribe or family were under-represented. Moreover, they were able to show statistically that, in the case of *D. quadrijuga* being tested for the control of *H. amplexicaule*, this added no extra information upon which to assess risk (Briese & Walker, 2002). They suggested that selection of test plants based on phylogeny *sensu strictu* would lead to less unnecessary testing of more distant plant taxa and concentrate the measurement of host-choice responses on the phylogenetically closer and more informative plant lineages.

Component B – safeguard criteria

i) cultivated plants botanically related to the target weed

It is unclear why this is included as a safeguard, as it is merely an extension of the phylogenetic selection principal applied to a subset of plants. If the cultivated plant is closely related to the target weed, this is ample justification for choosing it under component A of Wapshere's (1974) selection process. Indeed, it makes sense, from a risk assessment perspective, to select economically or ecologically important plant species from among the many phylogenetically equidistant possibilities, rather than obscure species.

ii) cultivated plants for which there is little or no entomological or mycological knowledge

This criterion is to some extent self-contradictory. If such plants are related to the target-weed they would be selected under the previous criterion. If not related, inclusion of them would imply that the phylogenetic selection principal itself may be erroneous and would cast doubt on the whole process. In practice, criteria i) and ii) have generally been lumped together, as there are extremely few examples of cultivated plants that have a poorly known entomofauna or mycoflora.

iii) cultivated plants which have evolved apart, or which for geographic or climatic reasons have not been extensively exposed to the candidate agent (uncertainty of behaviour of agent faced with new potential host)

Recent evidence suggests that, where related plants have evolved apart, they are less likely to serve as hosts, because of divergent selection in characteristics that provide host-cues to the insects. The example of the genus *Heliotropium* mentioned earlier, in which Australian "*Heliotropium*" that had evolved apart were not recognised as host plants by a specialist phytophage of South American *Heliotropium* species, illustrates this. Moreover, endemic African *Solanum*-feeding insects do not appear to have colonised the introduced weed, *Solanum mauritianum* in South Africa to any great extent (Olckers & Hulley, 1991), providing complementary evidence that the evolution of geographic separated plant species is more likely to lead to divergent evolution of their specialist natural enemies and reduced risk of subsequent colonisation by these should they encounter the novel congeneric non-target species in a new habitat.

If the agent were not a specialist, then this would be discovered as a consequence of normal testing under component A of the CPM. In either case, it is not clear why such safeguard species need to be included.

iv) cultivated plants known to be attacked by organisms closely related to the candidate agent

It is a requirement of the importation permit to provide documentation of the host-range of close relatives to the candidate agent. However, the usefulness of this information for selecting test plants is not very clear, since there are many large insect genera which contain species that specialise on one or a few plants, but in quite different plant families, e.g. *Chrysolina* (Garin *et al.*, 1999) and *Longitarsus* (Dobler, 2001). In the case of *Chrysolina*, a well-known source of successful biological control agents for *Hypericum perforatum*, this criterion would have required testing candidate agents against species of Asteraceae, Apiaceae, Scrophulariaceae, Plantaginaceae and Lamiaceae, without changing the ultimate test result that the insects were specific to the genus *Hypericum* (Clusiaceae).

The phylogenetic data indicate that the host associations of "close relatives" are not particularly informative for the selection of test plants, as these large insect genera contain several lineages that often correlate with shifts to new plant families. Moreover, the host associations of congeneric species within the same phylogenetic lineage are more likely to reinforce evidence of host plant restriction, as Wapshere (1974) himself realised when playing down the importance of this criterion. It is clear, though, that a phylogenetic approach, rather than reliance on taxonomic circumscription, is equally important in the case of the phytophagous insects themselves as for their host plants.

v) any plants on which the candidate agent has been previously recorded

It is essential to test the veracity of literature records, either by confirmatory field observations in the native range during the exploration phase or by experiment if these differ from current field observations. Many such records are associated with taxonomic literature and often involve adult collection records where the insect may not even have been feeding. Such information would normally be obtained prior to seeking approval for formal host-specificity testing. True polyphages would be eliminated at this stage, and stenophagous agents with unacceptably broad ranges would be detected thorough normal application of the centrifugal-phylogenetic method.

Using safeguard species in practice

Most of the concerns of these safeguard criteria can be catered for by a strictly phylogenetically based test plant selection process. However, there remains the slight possibility that the species may be a disjunct oligophage, which would not necessarily be detected. Reported cases of such disjunct host-associations (e.g. Thompson, 1993; Gomez-Zurita *et al.*, 2000) suggest that this may not be due to true host restriction, but is geographically linked and dependent on the availability of different host-plants. Such species may thus not be true host specialists and could have much broader fundamental than realised host-ranges. While this poses a concern, an ability to develop on a broader range of plants should be still detected by strict phylogenetically-based testing. However, in some insect groups, there is a closer phylogenetic association with particular plant chemistries, than with overall plant phylogeny (e.g. Becerra, 1997). If disjunction in host usage is due to such an association, one case for which a "safeguard" plant selection may still be required would involve agents from insect taxa known to be associated with particular plant chemistries.

Ultimately, the value of the safeguard criteria must be judged by their effectiveness. How many potential biological control agents are there that have been rejected because of testing against a safeguard test plant, but would not have been rejected when tested solely against plant species selected on phylogenetic principles? This is a difficult question to answer as few cases of agent rejection are published. However, those published suggest that species selected uniquely on safeguard criteria have not played a role in rejection (e.g. McFadyen & Wegler-Beaton, 2000).

The case of *Microthrix inconspicuella*, a candidate agent for *Emex australis* (Polygonaceae), is instructive in this regard. This moth was originally rejected by Harley *et al.* (1979) because of significant larval feeding on apple (Rosaceae). However, subsequent testing by Shepherd (1990a) showed that *M. inconspicuella* could not complete its life-cycle on apple, though it was ultimately not introduced into Australia because the host-range within the Polygonaceae was found to be too broad (Shepherd, 1990b). In this case, testing the safeguard species, apple, proved to be a "red herring", while selection of test plants based solely on phylogenetic relatedness would have been sufficient to show that the risk of introduction was unacceptably high.

Palmer & Tomley (1993) rejected a cerambycid beetle tested for the biological control of *Baccharis halimifolia* (Asteraceae) in Australia because, although oviposition and larval feeding were restricted to *Baccharis*, adults fed on green bark from a wide range of plants in several families including distant economic crops such as citrus (Rutaceae). However, the broad range in adult feeding was evident from plants tested within the Asteraceae, suggesting that strict phylogenetic testing would have raised the same doubts about the range of adult feeding. Adult feeding is much more restricted in the field in its native range (Palmer & Tomley, 1993), indicating that the issue here, and many ambiguous cases, is more to do with the types of tests used and interpretation of test data rather than the use or not of safeguard species.

Recently, Briese & Walker (2002) carried out a statistical analysis of plant categories used for testing a candidate control agent for *Heliotropium amplexicaule*, and found that the key parameters measured (i.e. feeding, survival and oviposition of the chrysomelid beetle) decreased with increasing phylogenetic distance from the target weed, as expected, while the addition of safeguard species contributed no additional information about the host-range of the agent (Figure 1). The prevailing evidence therefore suggests safeguard criteria have little value in determining the risk of a candidate biological control agent to non-target species.

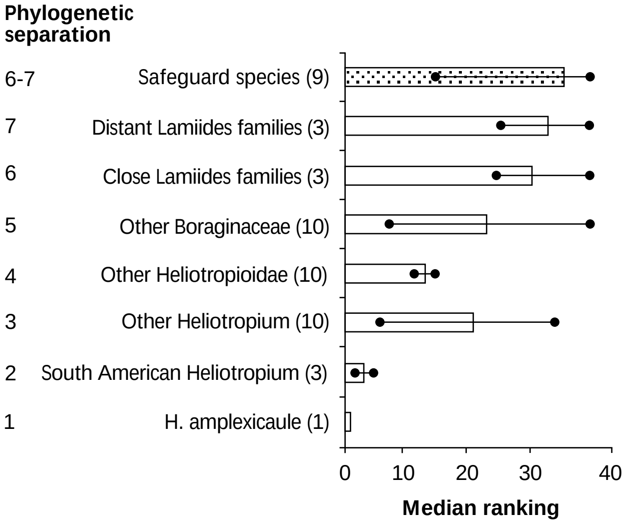

Figure 1. Median rankings of suitability as a host-plant for *Deuterocampta quadrijuga* of test plants with increasing degrees of phylogenetic separation from the target weed, *H. amplexicaule*. Bars indicate the range in rankings and bracketed figures show the number of tested species in each grouping (after Briese & Walker, 2002). N.B. One of the two "Other Heliotropioidae" belongs to the genus *Tournefortia*, which has been found to be paraphyletic within the South American *Heliotropium* (Gottschling et al., 2001), and which may explain its higher suitability ranking.

Modernising the centrifugal phylogenetic method?

The CPM has stood biological control practitioners in good stead for the past 28 years. There have been no "failures" due to the method, and, where controversy over biological control safety has occurred, it is invariably due to the interpretation and judgments based on testing data, i.e. where scientific data indicated that certain non-target impact was likely, political judgements were still made to release particular agents on the basis of potential benefits outweighing risks (e.g. Gassman & Louda, 2000). Wapshere (1974) based the CPM on two premises. His first component, the sequence for testing from more to less closely related organisms, was based on existing knowledge about the way in which insects choose their hosts. His second component, the safeguard criteria, was based on known gaps in this knowledge. It is worth examining to what extent these gaps have been filled and how the explosion of knowledge of plant phylogenetic relationships might affect the way in which we apply the CPM. With the development of a range of molecular markers, there has been a revolution in the study plan phylogenetic relationships over the past decade. Prior to 1990 there were very few papers on the subject, but since then almost 1000 papers have been published and the number is increasing each year (Figure 2). Of the 42 plant families represented in Julien & Griffith's (1998) most recent catalogue of weed biological control projects, 39 have been subject, in whole or in part, to phylogenetic analysis (ISI Web of Science® database). Thus there is an enormous source of new information that might be applied to the selection of test plant species.

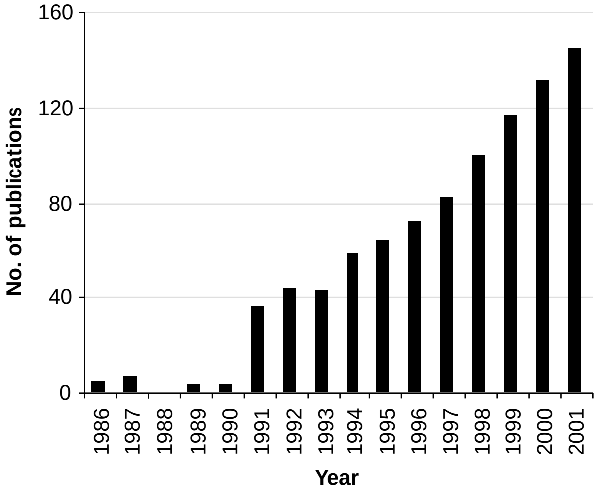

Figure 2. The number of publications concerning the phylogenetic relationships of plants since 1986 (based on a search of the ISI Web of Science® database).

To decide how we can best advance the process, it is instructive to revisit the basic tenets of host-specificity testing. The primary purpose of doing this is to satisfy regulatory authorities, who act on behalf of the general public, that any proposed agent introductions will not have an unacceptable impact, either ecological or economic, on the environment into which it is being introduced. Today, the activities of regulatory authorities are couched in terms of risk. For example, the role of Biosecurity Australia, as it relates to biological control, is to "assess the quarantine risks associated with import proposals for animals and plants and their products". Therefore, if we are to modernise the centrifugal-phylogenetic, it needs to be done within the framework of risk assessment, rather than being couched in terms of "safety".

Lonsdale *et al.* (2000) recently examined the application of risk analysis to weed biological control. They argued that biological control practitioners needed first to identify the risks, that these identified risks need to be measured, an estimate of their extent (i.e. biogeographic limits) made and the risk characterised by interpreting the data available from these processes. There are three major components of risk in the case of weed biological control. Firstly, there is a risk that plant species other than the target weed may be colonised by the agent. This may have widespread, long-term population consequences and irreversible evolutionary consequences for the attacked plant, e.g. native North American cacti (Johnson and Stiling, 1996) and thistles (Louda, 2000). Secondly there is a risk that, even though the agent cannot complete its life-cycle on a non-target plant, there may be some collateral damage if the agent feeds on it at any particular stage. Such effects are usually only localised and temporary. Nevertheless, while population consequences to the plant would be short-term and reversible, this may lead to unacceptable economic impacts (e.g. the occasional damage of sunflower crops by the introduced parthenium leaf-beetle, *Zygogramma bicolorata*, (Withers, 1998) or "spillover" feeding on non-target plants by teneral adults of the purple loosestrife leaf-beetle, *Galerucella calmiensis* (Blossey *et al.*, 2001). Host-specificity testing procedure needs to examine and report on both these components. Finally, there may be a risk of broader indirect flow-on effects through competitive and trophic interactions due to the presence of a new organism in locally high numbers (Strong & Pemberton, 2000). At the present time, this risk is speculative and it is not possible to measure it prior to release of the agent. It therefore cannot form part of a formal testing procedure.

For the first two components, the risk posed by an introduced agent to a novel flora may vary from none to very high. The selection of a test list is necessary only because we cannot logistically test every plant potentially at risk, and a process is needed to enable risk to be accurately estimated within practical limitations. Briese & Walker (2002) have suggested that the measurement of such potential risk can be facilitated by breaking it down into three contributory elements; phylogenetic relatedness, biogeographic overlap and ecological similarity (Figure 3), which define the criteria used to select plants for assessing the risk of non-target impact As indicated earlier, the arguments put forward by Wapshere (1974) still hold, and the phylogenetic relationships of plants provides the strongest indicator of the complex behavioural and physiological responses shown by specialist phytophages in choosing a host plant. This means that phylogeny *sensu strictu* must remain the key criterion used to choose test plants.

Briese *et al.* (2002) proposed the idea of grouping test plants into phylogenetic clades increasingly distant from the target weed, rather than into named taxa. This more accurately reflects the relationships of test plants to the target weed. Results based on phylogenetic relationships also more accurately reflect the degree of host-specialisation (Symons & Beccaloni, 1999), e.g. an agent may feed on two genera of plants within a family, but, if the genera are in sister clades, the agent would be more specialised than if they belong to more divergent phylogenetic lineages. Figure 4 shows that grouping

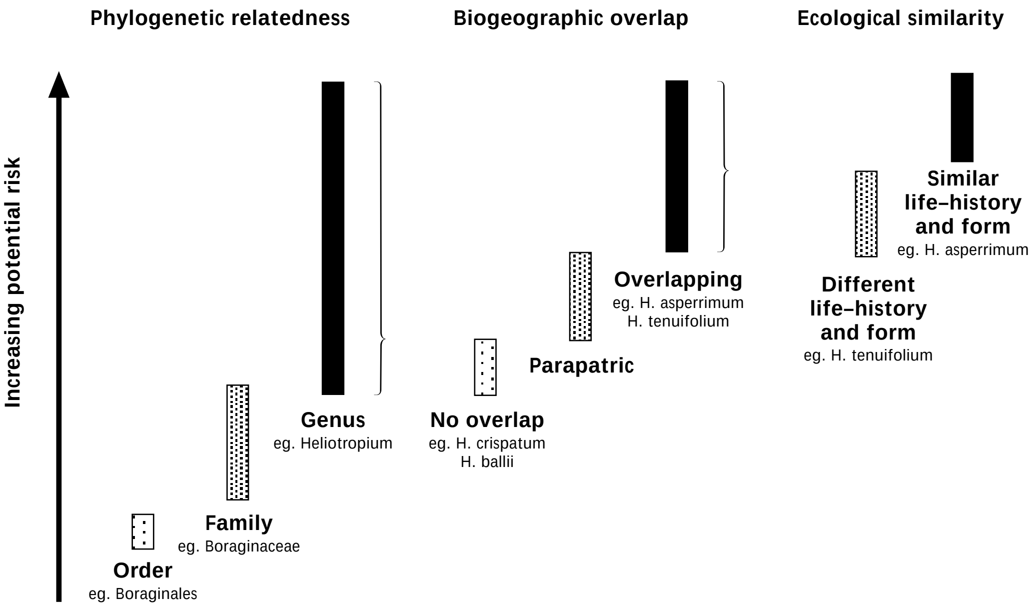

Figure 3. The relativity of potential risk to non-target plant species based on phylogeny, biogeography and ecology. The testing procedure should seek to measure the maximum risk posed by an agent's introduction. Actual measured risk may be much lower than potential risk, but the latter provides a useful framework for selecting test plants (using *Heliotropium amplexicaule* as an example target weed after Briese & Walker, 2002).

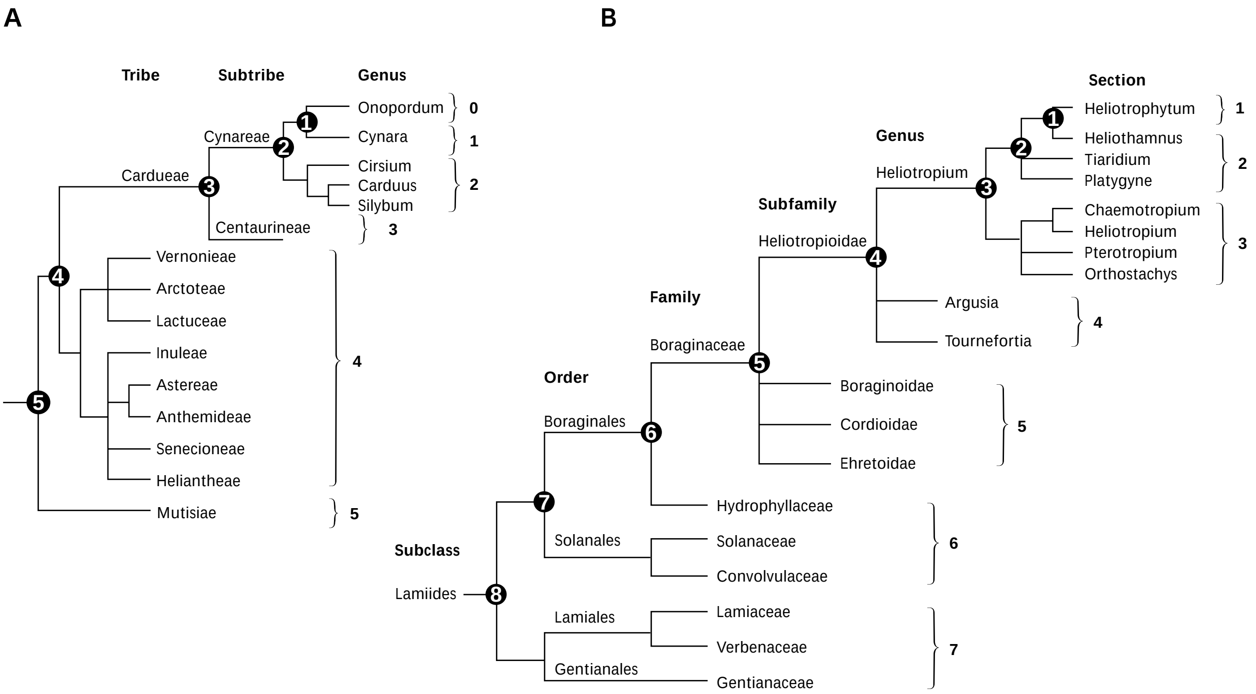

Figure 4. Phylogenetic relationships of A) representative Asteraceae taxa used for host-specificity testing of candidate agents for the biological control of *Onopordum* spp (from Briese *et al.*, 2002) and B) Boraginaceae and related taxa used for host-specificity test of candidate agents for the biological control of *Heliotropium amplexicaule* (from Briese & Walker, 2002). Numbered circles indicate nodes where lineages diverge while the numbers on the right show clades with increasing degrees of separation from the target weed. The higher the degree of separation, the fewer species would be tested from each clade, e.g. in A) 15 named taxa (genera, subtribes and tribes) were represented during testing, though there are only 5 degrees of separation. Instead of a representative from each Asteraceae tribe, the test list need only include 1-2 representatives from each of the two most distant clades. Similarly, in B) 19 named taxa (from section to order) were represented during testing, with only 8 degrees of separation. However, this included 3 infrageneric degrees of separation within *Heliotropium*. More species would therefore be tested in more closely related and fewer species tested in less related groups than if selection were based solely on named taxa.

plants into phylogenetic clades can substantially alter the number of classes of plants that need to be tested, since several named taxa may be equivalent in their degree of separation or a single taxon may have more than one degree of separation.

The measurement of risk to non-target flora can be further refined by limiting testing to those phylogenetically related plants for which there is potential biogeographic overlap with the candidate agent (Figure 3). This can be determined from data collected on the agent during the survey phase of a biological control project and by using climate-matching models such as CLIMEX or BIOCLIM to predict suitable ranges for the agent in its new habitat (e.g. Maywald & Sutherst, 1999). This criterion also addresses the issue of measuring the extent of risk that Lonsdale *et al.* (2000) considered important to the assessment process.

Finally, as mentioned earlier, host-association is mediated by ecological and phenological adaptations that ensure that the phytophage's life-cycle is in synchrony with that of its host. Hence, a third refinement to the assessment of potential risk can be made via an ecological criterion, in which phylogenetically related and biogeographically overlapping plant species are selected on the basis of similarity in life-history and phenological traits that may be necessary for the agent to complete its life-cycle (Figure 3). Careful selection of test plants on the basis of these three criteria will identify species with the highest "host potential" for the candidate agent, ensuring that subsequent measurements will provide the most reliable assessment of actual risk. It should be noted that the biogeographic and ecological criteria are not mandatory, but are available to reduce the large number of species that may fall into one particular phylogenetic distance class into a manageable number comprising those plants at highest risk of impact from the candidate agent. It is also not critical in which order these two criteria are applied, as their combined filtering effect would be the same. Finally, economically or ecologically important plant species that satisfy these criteria should be selected over more obscure species that might be judged to have equal "host potential". Once scientific criteria have been met, there is scope for political pragmatism.

Discussion

The centrifugal phylogenetic method was appropriate for its time, given the state of knowledge of plant-insect relationships at the time. However, it is clear that recent advances in this knowledge would enable a modernisation of the way in which we select plants for host-specificity testing of weed biological control agents. Any changes, though, would need to be both scientifically acceptable and politically palatable. The model proposed here attempts to do this by deliberately framing the way testing is done in the language of risk assessment, which is the current way in which regulators look at activities such as biological control. Moreover, it makes use of recent advances in plant phylogeny by basing test plant selection on representative clades with measurable degrees of phylogenetic separation from the target weed, instead of named hierarchical taxa that may or may not accurately reflect evolution of the plants in question. Finally, it recommends abandonment of the practice of including safeguard species that have no phylogenetic justification.

Regulatory policies with respect to biological control around the world are becoming more stringent. For example, in North America it would be no longer possible to release insects, such as *Rhinocyllus conicus*, for the control of introduced weedy thistle species, when their host range includes endemic North American thistle species. The leaf-mining moth, *Dialectica scalariella*, which can develop on a number of boraginaceous genera was authorised for release for the control of *Echium* spp. in Australia 20 years ago, but would almost certainly not be permitted to be released today. It thus becomes increasingly important to focus on host-usage at narrower rather than broader limits, as this is most likely to reflect actual risks. One feature of using phylogenetic clades rather than named taxa as the basis for selecting test plants is that it directs attention to closer clades and away from more distantly related plants. It is therefore more in tune with the current stringent regulatory policy.

Briese & Walker (2002) tested this model with *Deuterocampta quadrijuga*, a leaf-feeding chrysomelid beetle, proposed for the control of *Heliotropium amplexicaule* in eastern Australia. Phylogenetic examination indicated that the plants at greatest risk were indigenous species of *Heliotropium*. As there were over 70 such species (Craven, 1996), the list was refined to include the seven species considered most a risk to this particular introduced leaf-beetle, based on the biogeographic and ecological filters. The rationale for doing this was clearly explained and was apparently acceptable to Biosecurity Australia and other reviewing agencies, as this part of the test list was approved. However, Biosecurity Australia did not accept the absence of safeguard economic species from the test list, even though other members of those plant taxa were included. Hence nine such species had to be added to the list and tested. As mentioned earlier, the host-range determined and the assessment of risk was the same, with or without the economic test plants.

This demonstrates that the effective communication of risk and the way it is measured is a critical part of the process (see Lonsdale *et al.*, 2000). If biological control practitioners invoke changes in the way that test plants are selected, it should be done in collaboration with the regulatory authorities rather than being presented to them as a *fait accompli* for endorsement. The scientific and political aspects of biological control cannot be divorced, and it is critical that there not only be consensus amongst scientists on how testing should be done, but that there be consensus between the scientists and policy makers.

Finally, it is important to place the CPM in context. It is only the first stage of the host-specificity testing process, which involves 1) what plant species should be tested, 2) what life-stages of the agent should be tested against them, 3) what types of test should be used for these life-stages and 4) how the data arising from these tests should be interpreted to best reflect the different risk components that would follow their introduction. The way in which test plants are selected loses its relevance if there are flaws in these latter stages. The recent workshop held under the auspices of the CRC for Tropical Pest Management (see Withers *et al.*, 1999) has contributed to development of a consensus on the methodology and interpretation of testing, but the selection of test plant was not considered at the time. It is hoped that the ideas put forward in this paper will stimulate a debate on the way test plants are selected in weed biological control. The CRC for Australian Weed Management Systems now has the opportunity to do this and to develop a complete set of guidelines on all stages of the testing process, acceptable to both biological control practitioners and biosecurity regulators.

References

Becerra, J.X. (1997) Insects on plants: Macroevolutionary trends in host use. *Science* **276**, 253-256.

Bernays, E.A. (2000) Neural limitations in phytophagous insects: Implications for diet breadth & evolution of host affiliation. *Annual Review of Entomology* **46**, 703-727.

Blossey, B., Casagrande, R., Tewksbury, L., Landis, D.A., Wiedenmann, R.N. & Ellis, D.R. (2001) Nontarget feeding of leaf-beetles introduced to control purple loosestrife (*Lythrum salicaria L.*). *Natural Areas Journal* **21**, 368-377.

Briese, D.T. (1996) Phylogeny: can it us to help understand host-choice by biological control agents? In *Proceedings of the 9th Symposium on the Biological Control of Weeds* (V.C. Moran, & J.H. Hoffman, Eds), pp 63-70, UCT, Cape Town.

Briese, D.T. & Walker, A. (2002) A new perspective on the selection of test plants for evaluating the host-specificity of weed biological control agents: The case of *Deuterocampta quadrijuga*, a potential insect control agent of *Heliotropium amplexicaule. Biological Control* **25**, 273-287.

Briese, D.T., Walker, A., Pettit, W. & Sagliocco, J-L. (2002) Host-specificity of candidate agents for *Onopordum* spp. thistles in Australia: An assessment of testing procedures. *Biocontrol Science & Technology* **12**, 149-163.

Craven, L. (1996) A taxonomic revision of *Heliotropium* (Boraginaceae) in Australia. *Australian Systematic Botany* **9**, 521-657.

Dobler, S. (2001) Evolutionary aspects of defence by recycled plant compounds in herbivorous insects. *Basic & Applied Ecology* **2**, 15-26.

Dodd, A.P. (1940) *The Biological Campaign Against Prickly Pear*. Commonwealth Prickly Pear Board, Brisbane.

Forno, W. & Heard, T. (1997) Compiling a plant list for testing the host range of agents. *In Biological Control of Weeds: Theory & Application* (M. Julien & G. White, Eds), pp 71-76, ACIAR, Canberra.

Futuyma, D.J. (2000) Potential evolution of host range in herbivorous insects. *In Host-Specificity Testing of Exotic Arthropod Biological Control Agents – the Biological Basis for Improvement in Safety*, (R. van Driesche, T.A. Heard, A.S. McClay & R. Reardon, Eds), pp 42-53, USDA Forestry Service Publication FHTET-99-1.

Garin, C.F., Juan, C. & Petitpierre, E. (1999) Mitochondrial DNA phylogeny & the evolution of host-plant use in palearctic *Chrysolina* (Coleoptera : Chrysomelidae) leaf beetles. *Journal of Molecular Evolution* **48**, 435-444.

Gassmann, A. & Louda, S.M. (2000) *Rhinocyllus conicus:* Initial evaluation & subsequent ecological impacts in North America. In *Evaluating Indirect Ecological Effect of Biological Control* (E. Wajnberg, J.K. Scott & P.C. Quimby, Eds), pp 147-183, CABI Publishing, Wallingford.

Gomez-Zurita, J. Petitpierre, E. & Juan, C. (2000) Nested cladistic analysis, phylogeography & speciation in the *Timarcha goettingensis* complex (Coleoptera: Chrysomelidae). *Molecular Ecology* **9**, 557-570.

Gottschling, M., Hilger, H.H., Wolf, M. & Diane, N. (2001) Secondary structure of the ITS1 transcript & its application in a reconstruction of the phylogeny of Boraginales. *Plant Biology* **3**, 629-636.

Harley, K.L.S., Kassulke, R.C. & Julien, MH. (1979) Biology & host-specificity of *Microthrix inconspicuella* (Lepidoptera: Pyralidae), a natural enemy of *Emex australis* in South Africa. *Journal of the Entomological Society of South Africa* **42**, 343-348.

Harris, P. (1998) Evolution of classical weed biocontrol: Meeting survival challenges. *Bulletin of the Ecological Society of Canada* **30**, 134-143.

Harris, P. & McEvoy, P. (1995) The predictability of insect host plant utilisation from feeding tests & suggested improvements for screening weed biological control agents. In *Proceedings of the 8th Symposium on the Biological Control of Weeds, Lincoln, February 1992* (E.S. Delfosse & R.R. Scott, Eds.), pp 125-131, CSIRO Publishing, Melbourne.

Harris, P. & Zwölfer, H. (1968) Screening of phytophagous insects for the biological control of weeds. *Canadian Entomologist* **100**, 295-303.

Howarth, F.G. (1983) Classical biocontrol: panacea or Pandora's box. *Proceedings of the Hawaiian Entomological Society* **24**, 234-244.

Huffaker, C.B. (1957) Fundamentals of biological control of weeds. *Hilgardia* **27**, 101-107.

Johnson, D.M. & Stiling, P.D. (1996) Host specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an *exotic Opuntia*-feeding moth, in Florida. *Environmental Entomologist* **25**, 743-748.

Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds: A World Catalogue of Agents & Their Target Weeds, 4th Edition*, CABI, Wallingford.

Lonsdale, W.M., Briese, D.T. & Cullen, J.M. (2000) Risk analysis & weed biological control. In *Evaluating Indirect Ecological Effects of Biological Control.* (Wajnberg, E., Scott, J.K. & Quimby, P.C., Eds), pp 185-210, CABI, Wallingford.

Louda, S.M. (2000) Negative ecological effects of the musk thistle biological control agent, *Rhinocyllus conicus.* In *Nontarget Effects of Biological Control* (P.A. Follet & J.J. Duan, Eds), pp214-244, Kluwer Academic, Boston.

Maywald, G. & Sutherst, R. (1999) Climate matching using the CLIMEX program. In *Biological Control of Weeds: Theory & Application* (M. Julien & G. White, Eds), pp. 165-176. ACIAR, Canberra.

McFadyen, R.E. & Weggler-Beaton, K. (2000) The biology & host-specificity of *Liothrips* sp. (Thysanoptera: Phlaeothripidae), an agent rejected for biocontrol of annual ragweed. *Biological Control* **19**, 105-111.

Miller, J.T. & Bayer, R.J. (2001) Molecular phylogenetics of *Acacia* (Fabaceae: Mimosoidae) based on the chloroplast MATK coding sequence & flanking TRNK intron spacer regions. *American Journal of Botany* **88,** 697-705.

Mishler, B.D. (1999) Getting rid of species? In *Species: New Interdisciplinary Essays* (R.A. Wilson, Ed.), pp.304-315, MIT Press, Cambridge.

Mitter C., Farrell B. & Futuyma D.J. (1991) Phylogenetic studies of insect-plant interactions: Insights into the genesis of diversity. *Trends in Ecology & Evolution*, **6**, 290-293.

Olckers, T. & Hulley, P.E. (1991) Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/KwaZulu & the Transkei. *Journal of the Entomological Society of Southern Africa* **54**, 39-50.

Palmer, W.A. & Tomley, A.J. (1993) The host range & biology of *Amniscus perplexyus* Haldeman (Coleoptera: Cerambycidae), a candidate evaluated for the biological control of *Baccharis halimifolia* in Australia. *Coleopterist's Bulletin* **47**, 27-34.

Pemberton, R.W. (2000) Predictable risks to native plants in weed biological control. *Oecologia* **25**, 489-494.

Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology* **77**, 1965-1974.

Shepherd, R.C.H. (1990a) Evaluation of *Microthrix inconspicuella* (Lepidoptera: Pyralidae), a potential biological control agent of *Emex australis* in Australia, carried out in apple orchards in South Africa. *Entomophaga* **35**, 583-587.

Shepherd, R.C.H. (1990b) Past Victorian work on *Emex australis* Stenheil & *Tribulus terrestris L. Plant Protection Quarterly* **5**, 100-102.

Strong, D.R. (1997) Fear no weevil? *Science* **277**, 1058-1059.

Strong, D.R. & Pemberton, R.W. (2000) Food webs, risk of alien enemies & reform of biological control. In *Evaluating Indirect Ecological Effects of Biological Control.* (Wajnberg, E., Scott, J.K. & Quimby, P.C., Eds), pp 57-80, CABI, Wallingford.

Symons, F.B. & Beccaloni, G.W. (1999) Phylogenetic indices for measuring the diet breadths of phytophagous insects. *Oecologia* **119**, 427-434.

Thompson, J.N. (1993) Preference hierarchies & the origin of geographic specialization in host use in swallowtail butterflies. *Evolution* **47**, 1585-1594.

van Driesche, R., Heard, T.A., McClay, A.S. & Reardon, R. (2000) *Host-Specificity Testing of Exotic Arthropod Biological Control Agents – the Biological Basis for Improvement in Safety*. USDA Forestry Service Publication FHTET-99-1.

Wapshere, A.J. (1974) A strategy for evaluating the safety of organisms for biological weed control. *Annals of applied Biolog*y **77**, 20-211.

Withers, T.M. (1998) Influence of plant species on host acceptance behavior of the biocontrol agent *Zygogramma bicolorata* (Col.: Chrysomelidae). *Biological Control* **13**, 55-62.

Withers, T.M., Barton Browne, L. & Stanley, J. (1999) *Host-Specificity Testing in Australasia: Towards Improved Assays for Biological Control*. Scientific Publishing, Indooroopilly.

Zwölfer, H. & Harris, P. (1971) Host-specificity determination of insects for biological control of weeds. *Annual Review of Entomology* **16**, 159-178.

Predictability and acceptability: Potential for damage to non-target native plant species by biological control agents for weeds

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Summary

Screening procedures for host-specificity of biological weed control agents attempt to limit the possibility that agents will affect non-target species, especially those having some economic benefit. There remains concern, however, about potential adverse environmental effects from agents released for biological control, particularly when target weeds are related to rare or endangered native plant species. We collated information from past weed biocontrol programs in Australia to identify agents that had been approved for release even though testing indicated that certain native species may be attacked. We aimed, thereby, to begin the process of assessing the safety of biological weed control in Australia. We identified a total of 17 agents targeted against 9 weed species with potential to attack at least 30 native species. Our data imply that glasshouse-based predictions of attacks on non-target species are accurate, thereby confirming the rigour of current screening procedures for host-specificity. However, there appears to have been only one published field-based evaluation of the impact of weed biocontrol agents on native plants in Australia; *Aculus hyperici*, targeted at *Hypericum perforatum*, on *H. gramineum*. More post-release studies are required to demonstrate the accuracy of glasshouse predictions and to evaluate the significance of any damage that may be caused; we highlight four such studies that are needed particularly urgently. Biological weed control in Australia appears to have a good safety record in terms of impacts on non-target species and hence, native plant diversity, but a general lack of post-release evaluations means that this conclusion is drawn with caution.

Key words: non-target impact, host selection

Introduction

Current screening procedures for potential biological control agents for weeds attempt to limit the possibility that agents selected for field-release will affect non-target species, especially those having some economic benefit. There remain concerns, however, about potential adverse impacts of agents on native species. Such concerns were highlighted recently by the case of *Rhinocyllus conicus*, which was introduced to North America to help control introduced thistle species and, since then, has been found attacking non-target native American thistles and affecting species elsewhere in the food web associated with the native plants (Louda, 1998; Louda *et al.*, 1997).

Clearly, the impact on non-target native species of *R. conicus*, among other examples (Diehl & McEvoy, 1990; Johnson & Stiling, 1996, 1998), challenges the 'green' image of biological weed control (Simberloff & Stiling, 1996a, b). Advocates of biocontrol argue that impacts on non-target species are relatively rare and that the benefits of control usually outweigh risks. Critics note, however, that few studies specifically investigate the frequency or scale of impacts on non-target species (Simberloff & Stiling, 1996a, b).

Currently, it is difficult to assess the 'track record' of Australia in biological weed control in relation to impacts on non-target native species. The difficulty reflects both a paucity of post-release studies on non-target species as well as challenges in accessing the information that does exist — relevant information is usually collected during pre-release host-specificity trials conducted in quarantine conditions, but is published comparatively rarely; government agencies entrusted with relevant information do not allow ready access to the data; and the anecdotal accounts and experience of biocontrol practitioners are difficult to obtain.

Despite these challenges, these types of information have clear potential to inform the current debate about the safety of biological weed control. A broad objective of this study, therefore, was to locate and synthesise such information, to begin the process of investigating the impacts of Australia's biological weed control programs on native flora. Specifically, we aimed to determine the native plant species at greatest risk of being used as alternative hosts by biocontrol agents and to evaluate the threat posed by the agent(s) to the native(s), based on the available information. The study does not imply that such natives are actually being harmed by the agents, since determining whether non-target species are significantly harmed requires empirical field studies that quantify the impact of the agent on some measure of growth (Hopper, 2000; Pemberton, 2000). We hope, however, that the results of this project will focus empirical field research on the species most likely to be harmed, so that the actual impact on native species can be assessed accurately and compared with pre-release predictions about the safety of agents. Such empirical studies should help to redress the current inconsistency between stringent requirements for detailed host-specificity testing in quarantine pre-release, and the relative lack of post-release monitoring for potential impacts on non-target species.

Methods

We collated available information on weed control agents that were released in Australia till 1996 (Julien & Griffiths, 1998), despite feeding, surviving and reproducing on taxonomically related native species during quarantine-based host-specificity feeding trials. We are aware that several agents have been released since then, but inclusion of these was beyond the scope of the current project. Although the use of non-target species by potential agents does not, necessarily, imply a significant impact on the non-target (see above; Pemberton, 2000; Turner, 1985), it provides an early indication of a potential impact. We limit our consideration to potential impacts on native species for two reasons. Firstly, impacts on non-target species of agricultural importance are likely to be observed soon after they occur and, therefore, are more likely to be reported formally elsewhere. Secondly, there is relatively less evaluation of potentially important biodiversity implications of biocontrol releases. Although quarantine trials do test for impacts against related native species, these are rarely reported in published literature and, even less frequently, evaluated in post-release studies.

Unfortunately, we were unable to access Government (Australian Quarantine Inspection Service) records of host-specificity tests for weed biocontrol agents that have been released in Australia. As with Pemberton (2000), therefore, our main sources of information were specialised literature (where available) supplemented by personal communications from researchers familiar with specific biocontrol projects. In this regard, we contacted researchers in each of the major Australian agencies conducting biological weed control (CSIRO Entomology; Victorian Department of Natural Resources and Environment (Keith Turnbull Research Institute); Queensland Department of Natural Resources and Mines (Alan Fletcher Research Institute and Tropical Weeds Research Centre); Western Australian Department of Agriculture, and the Tasmanian Institute of Agricultural Research). Case studies suggested by these scientists were used as the basis of this project.

The distributions of potentially impacted native plants in relation to those of relevant target weeds were obtained from State and federal government herbarium records. Any overlap in the geographical distribution of non-target native and target weed species provided an initial indication of the likelihood that an agent would encounter, and potentially use, a native as an alternative host plant. We combined this initial map-based assessment of the potential use of non-target species with ecological information available in the literature to assess the threat posed to non-target native species by introduced biocontrol agents.

Results and discussion

Julien & Griffiths (1998) identified 164 individual species of biocontrol agent that have been released in Australia since the first agents introduced to control *Opuntia vulgaris* Miller and *Lantana camara* Linnaeus, in 1914. Although the taxonomy of at least nine of these species is uncertain (Julien & Griffiths, 1998), and it is possible that some introductions may not have been novel species, we considered each listing of an unidentified taxon to be a new introduction.

The 164 species introduced to Australia were targeted against a total of 53 weed species. About half (83) of the agents were introduced between 1980 and 1996. Most weeds have been targeted by more than one species of biocontrol agent. As an extreme example, 25 agents from 18 genera have been introduced to help control *Lantana camara*. Similarly, on occasions the same species of control agent has been targeted against several distinct, but related, weed species. *Hypogeococcus festerianus* (Lizer y Trelles), for instance, was introduced separately in 1975, 1976, 1979 and 1982 to help control each of *Harrisia martinii* (Labouret) Britton & Rose, *H. tortuosus* (Forbes) Britton & Rose, *Acanthocerus pentogonus* (Linnaeus) Britton & Rose and *H. bonplandii* (Parmentier) Britton & Rose (Cactaceae), respectively.

Of the 164 agents introduced to Australia, we identified 17 reported to have the potential to utilise native plant species as alternative hosts (Table 1). These agents were targeted against a total of nine weed species but may impact upon a total of at least 30 native species. It is noteworthy that the host-specificity testing of several of these 'threatening' agents was undertaken at a time when potential impacts on species of economic interest were considered to be of greater concern than such impacts on native plants. For example, in relation to the relatively broad host range of *Dialectica scalariella*, introduced to control *Echium plantagineum* (Table 1), Wapshere & Kirk (1977) argued that the benefits of introducing the moth outweighed any risks (including its potential to affect native Australian boraginaceous species, although none appear to have been tested; see Wapshere & Kirk (1977)), since "the five related plant genera that it attacks all belong to the Boraginaceae, and no member of this family is of importance in Australian agriculture". Fortunately, the attitudes of scientists, bureaucrats and the public to native biodiversity have matured. To this extent, it is possible that some widely established agents, both in Australia and elsewhere, would not have been released under the safety standards that are applied to weed biocontrol today (Harris & McEvoy, 1995).

In the following sections we describe the distribution of the nine weeds, highlighting regions of sympatry with related native species. We also discuss the potential for the biocontrol agents to colonise, and adversely affect, these alternative native hosts. It should be noted that, unless indicated otherwise, wherever we identified an agent as potentially damaging, its performance (feeding, oviposition, infection etc.) on the native(s) during host-specificity testing was consistently poorer than its performance on the target species. Universally, permission was granted to release the agent, despite potential to damage non-target species, based on assessments that the benefits of controlling the weed, outweighed the potential risks posed by the agents' release.

(1) *Cryptostegia grandiflora* (rubber vine: Asclepiadaceae)

Rubber vine is a native of Madagascar and a serious agricultural and environmental weed of north Queensland to where it has been introduced. It is confined to areas of tropical and sub-tropical Queensland with an annual rainfall of between 400-1400 mm.

Euclasta gigantalis was first introduced to help control rubber vine in 1988 (Julien & Griffiths, 1998), with its establishment confirmed in 1995 (Mo et al., 2000). Field releases of *E. gigantalis* were permitted, despite strong evidence that *Gymnanthera oblonga* was likely to be attacked by the agent. It was argued that in the absence of effective control, the native was likely to be competitively displaced by the weed, with local extinction over much of northern Queensland (McFadyen *et al.* 2002; McFadyen & Marohasy, 1990). Based on host-specificity tests, it is also possible that *E. gigantalis* may attack *G. cunninghamii*.

Rubber vine is broadly sympatric with *G. oblonga* throughout much of the weed's distribution in Queensland. Field observations confirm that locally the weed can inhabit similar environments to *G. oblonga* (coastal and riverine forests, mangrove edges and humid vine thickets (McFadyen & Marohasy, 1990). In these circumstances, *E. gigantalis* has been found feeding on the native, as predicted by the pre-release host-specificity tests (R. McFadyen, Alan Fletcher Research Station, pers. comm.), though only when larvae are also present and feeding on closely associated infestations of the weed (McFadyen *et al.* 2002). By contrast, the threat posed to *G. cunninghamii* by *E. gigantalis* is negligible, because of the large geographic distances that can separate populations of these species, with *G. cunninghamii* occurring in the deserts of central Australia, from Alice Springs west to the Kimberley (McFadyen & Marohasy, 1990). Consequently, we have assessed the risks posed by the agent *E. gigantalis* as being high for *G. oblonga* and low for *G. cunninghamii*.

(2) *Echium plantagineum* (Paterson's curse: Boraginaceae)

Echium plantagineum is indigenous to the regions around the western Mediterranean Sea. It occurs in all Australian States, but is most common in south-west Western Australia, central and southern New South Wales and Victoria.

Seven biocontrol agents have been introduced to Australia to help manage infestations of Paterson's curse, of which three – *Dialectica scalariella*, *Mogulones geographicus* and *Phytoecia coerulescens* – had established successfully by 1996 (Julien & Griffiths, 1998). Pre-release host-specificity testing of these agents occurred before the testing of native species closely related to the target weed became obligatory. Consequently, *Eucalyptus* and *Acacia*, genera of considerable commercial importance, were the only natives that were included in the tests (Kirk & Wapshere, 1979; Wapshere & Kirk, 1977), despite clear evidence that most members of the Boraginaceae are acceptable hosts for these agents.

Of the Australian Boraginaceae, *Cynoglossum australe, Myosotis australis* and *M. discolor* represent a number of herbaceous species of Boraginaceae at risk of attack by biocontrol agents for Paterson's curse, given their likely geographical overlap with the weed, and the relatively broad host range, within the Boraginaceae, of the agents.

Table 1. Australian weeds targeted for biological control by agents with known potential to attack non-target native Australian species. Each agent may attack each of the nominated native species associated with a given weed. In all cases, non-target natives are in the same family as the target weed with which they are associated.

Target weed	**Biocontrol agent(s)**	**Non-target native species**
Cryptostegia grandiflora (Roxburgh) R. Brown (Asclepiadaceae)	*Euclasta gigantalis* Viette (Lepidoptera: Pyralidae)	*Gymnanthera oblonga* (Burm.f.) P.S.Green *Gymnanthera cunninghamii* (Benth.) P.I.Forst.
Echium plantagineum Linnaeus (Boraginaceae)	*Dialectica scalariella* (Zeller) (Lepidoptera: Gracillariidae) *Mogulones geographicus* (Goeze) (Coleoptera: Curculionidae) *Phytoecia coerulescens* (Scopoli) (Coleoptera: Cerambycidae)	*Cynoglossum australe* R.Br. *Myosotis australis* R.Br. *Myosotis discolor* Pers.
Eichhornia crassipes (Martius) Solms-Laubach (Pontederiaceae)	*Xubida infusellus* (Walker) (Lepidoptera: Pyralidae)	*Monochoria australasica* Ridl. *Monochoria cyanea* (F.Muell.) F.Muell. *Monochoria hastata* (L.) Solms *Monochoria vaginalis* Kunth
Heliotropium europaeum Linnaeus (Boraginaceae)	*Uromyces heliotropii* Sred (fungus: Uredinales)	*Heliotropium crispatum* F.Muell. ex Benth.
Hypericum perforatum Linnaeus (Clusiaceae)	*Aculus hyperici* (Liro) (Acarina: Eriophyidae) *Aphis chloris* Koch (Hemiptera: Aphididae) *Chrysolina quadridgemina* (Suffrian) (Coleoptera: Chrysomelidae)	*Hypericum gramineum* G.Forst. *Hypericum japonicum* Thunb.
Mimosa pigra Linnaeus (Mimosaceae)	*Coelocephalapion pigrae* Kissinger (Coleoptera: Apionidae) *Neurostrota gunniella* (Busck) (Lepidoptera: Gracillariidae)	*Neptunia dimorphantha* Domin *Neptunia gracilis* Benth. *Neptunia major* (Benth.) Windler *Neptunia monosperma* F.Muell. ex Benth.
Rubus fruticosus Linnaeus, aggregate (Rosaceae)	*Phragmidium violaceum* (Schultz) Winter (fungus: Uredinales)	*Rubus gunnianus* Hook. *Rubus moorei* F.Muell.
Rumex pulcher Linnaeus (Polygonaceae)	*Synansphecia doryliformis* (Ochsenheimer) (Lepidoptera: Sesiidae)	*Rumex bidens* R.Br. *Rumex alcockii* Rech.f. *Rumex brownii* Campd. *Rumex crystallinus* Lange *Rumex drummondii* Meisn. *Rumex dumosus* Meisn. *Rumex stenoglottis* Rech.f. *Rumex tenax* Rech.f.
Senecio jacobaea Linnaeus (Asteraceae)	*Cochylis atricapitana* (Stephens) (Lepidoptera: Tortricidae) *Longitarsus flavicornis* (Stephens) (Coleoptera: Chrysomelidae) *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae) *Tyria jacobaeae* (Linnaeus) (Lepidoptera: Arctiidae)	*Senecio glomeratus* Poir. *Senecio lautus* Willd. *Senecio linearifolius* A.Rich. *Senecio quadridentatus* Labill.

Julien & Griffith (1998) refer to the attack on *Cynoglossum australe* by *P. coerulescens*. Moreover, Sheppard (A. Sheppard, CSIRO Entomology, pers. comm.) attempted to quantify experimentally the impacts of both *P. coerulescens* and *D. scalariella* on this native, relative to impacts on the target weed. Despite atypical attack rates on both the weed and the natives, the results suggested that any potential impacts on *C. australe* would be minimal.

One reason for the poor performance of *P. coerulescens* on *C. australe* may be that the beetle can only complete its life cycle on species such as *E. plantagineum* with a large stem that develops in spring or summer (Kirk & Wapshere, 1979), whereas the stem of *C. australe* is relatively thin. Another likely reason for the apparent lack of detrimental impacts of *P. coerulescens* on native Boraginaceae relates to its marginal impacts on the target weed. Sheppard (pers. comm.) indicates that the maturation of *P. coerulescens* larvae occurs too late in the season to significantly reduce the weed's seed production. Acceptable natives that have a prolonged seed production and/or maturation period may be at greater risk of impact than *E. plantagineum*, but this does not appear to be the case with either *C. australe* (Cunningham *et al.*, 1981) or any of the native *Myosotis* species (Jessop & Toelken, 1986).

In Australia, *Dialectica scalariella* typically has limited impacts on populations of *E. plantagineum*, despite completing 5-7 generations per year on the weed. The marginal impacts of *D. scalariella* on the target species, which can occur at particularly high densities (Grigulis *et al.*, 2001; Sheppard *et al.*, 2001), suggest that any impacts on non-target natives would also be minimal, particularly as populations of the natives are neither as dense nor as widespread as those of the weed. Sheppard (pers. comm.) suggests that the most likely impacts from this moth on affected Australian Boraginaceae would be as 'flow on' from nearby, dense infestations of the weed that host a high density of moth larvae. Any such potential impacts are likely to be most severe during periods of drought, when the agent's impact on Paterson's curse is maximal (Sheppard, 1996). Sheppard (pers. comm.) indicates that, at one site on the Mornington Peninsula in Victoria, it was not clear if leaf-mining damage on *C. australe*, was caused by *D. scalariella* or by native *Dialectica* species known to be present in the area.

We were able to find only limited information regarding the impact of *Mogulones geographicus* on Australian Boraginaceae. As with *P. coerulescens,* however, the physical size of these agents suggests that only natives with a sufficiently large stem/tap root would be affected (M. Smyth, CSIRO Entomology, pers. comm.), and this does not appear to be the case with the native Boraginaceae. In common with the other established agents for Paterson's curse, the potential impacts of *M. geographicus* on native species are likely to be limited, given the typically limited damage that these agents cause to the target weed (Julien & Griffiths, 1998). We, therefore, have assessed these agents as posing a low risk to native Boraginaceae.

(3) *Eichhornia crassipes* (water hyacinth: Pontederiaceae)

Water hyacinth is a floating aquatic herb that originated in the Amazon River basin of South America. In Australia, water hyacinth occurs in still or slow-moving freshwater bodies, and has been recorded from each of the mainland states but is particularly common in waterways of tropical and subtropical eastern Australia.

Since 1975, four biocontrol agents have been released in Australia to help control infestations of water hyacinth. With the exception of the moth, *Xubida infusellus*, the establishment of which is likely, but unconfirmed, (Julien & Griffiths, 1998), each of the agents established and dispersed widely after release. None of the three established agents is believed to impact on non-target native species.

The distribution of *E. crassipes* in Australia is sympatric with four native Australian species of *Monochoria* (Pontederiaceae; see Table 1) that potentially may be damaged by *X. infusellus*. During host-specificity testing, *X. infusellus* showed no clear oviposition preference between water hyacinth and either *M. vaginalis* or *M. cyanea*. Larvae were able to complete their development and damage both of these native species (Julien *et al.*, 2001). To some extent, these 'non-target impacts' were expected, since field observations of the moth in South America demonstrated that several species in the Pontederiaceae could support the reproduction and development of *X. infusellus*. For this reason, coupled with the clear potential for impacts on *M. vaginalis* and *M. cyanea*, it is highly likely that the remaining Australian *Monochoria* species, *M. hastata* and *M. australasica*, also would be suitable hosts for *X. infusellus*, although they are relatively isolated geographically from infestations of water hyacinth.

Despite a high potential for *X. infusellus* to damage native *Monochoria* species and an expectation that such damage will occur if water hyacinth grows in their vicinity (Julien *et al.*, 2001), it was considered that the moth would have minimal sustained impact on the native species. This expectation largely reflected the apparent population ecology of Australian *Monochoria* spp., which often inhabit temporarily flooded ditches and drains, where the seeds germinate rapidly in response to submergence following rain (Julien *et al.*, 2001). Plants then grow rapidly and produce large quantities of seed. Julien *et al.* (2001) suggest that *Monochoria* spp. probably rely on rapid seed set for maintenance of future generations. Such an ephemeral habit means that the natives are unlikely to sustain populations of *X. infusellus* throughout the year. If *Monochoria* populations are attacked, the impacts are likely to be insignificant on populations of the natives, because the time interval between the development of leaves large enough to support maturation of *X. infusellus* and seed set is too short for the agent to grow and significantly reduce seed production.

Permission to release *X. infusellus* in Australia was granted because it was considered that any impact on native species would be local, short term and unlikely to cause sustained damage (Julien *et al.*, 2001) due to the ecology of the native species. Significantly, it was also recognised that, in the absence of control, water hyacinth is likely to be more damaging to local populations of *Monochoria* than the agent, because of the weed's competitive ability to form dense and persistent monocultures on the surface of infested waterways. While it is clear that native *Monochoria* species are likely to be colonised by *X. infusellus* where the native species co-occur with the weed, in the longer term, the ecology of the native species is likely to limit any damage that they may sustain. Therefore, we assess the threat posed by *X. infusellus* to native *Monochoria* species as moderate.

(4) *Heliotropium europaeum* (common heliotrope: Boraginaceae)

Heliotropium europaeum is native to Mediterranean Europe and south-west Asia, but is weedy across most of southern Australia. *Uromyces heliotropii* Sred (Uredinales) is a rust fungus that was introduced from Turkey in 1991 (Julien & Griffiths, 1998). During host-specificity testing, Hasan *et al.* (1992) observed that the native, *H. crispatum*, could be infected by the rust, albeit at low levels relative to the target weed.

Approval was given to release *Uromyces heliotropii* despite the rust's ability to infect the native species and cause low levels of disease severity, because *H. crispatum* is isolated from most infestations of common heliotrope by at least 600 km. *Heliotropium crispatum* occurs in a climatic region of Western Australia that is unsuitable for the development of the rust (Hasan *et al.*, 1992). Prevailing winds in this region run from west to east, thereby discouraging the transmission of spores from infected populations of the weed northwards, to populations of *H. crispatum* (Hasan & Delfosse, 1995). Moreover, the contrasting phenologies of the target weed and *H. crispatum* are likely to preclude impacts on the native, since *H. europaeum* is a summer-growing annual, whereas *H. crispatum* is found only in winter (Hasan & Delfosse, 1995). The risk of *H. crispatum* populations being affected adversely by *U. heliotropii* clearly is very low.

(5) *Hypericum perforatum* (St. John's wort: Hypericaceae)

St. John's wort was deliberately introduced into the Bright region of north-eastern Victoria as a horticultural or herbal plant during the mid 1800s, but quickly became a naturalised invasive plant, spreading throughout southern Australia.

St. John's wort has been the subject of numerous biological control programs in Australia, but only four of the 10 agents that have been introduced have established widely (Julien & Griffiths, 1998). Three of these agents, *Chrysolina quadrigemina*, *Aculus hyperici* and *Aphis chloris*, potentially threaten native species since, during pre-release specificity testing, each fed and reproduced on *Hypericum gramineum* and, to a lesser extent, on *H. japonicum* (J. Cullen, unpublished; Briese, 1989; CSIRO, 1991).

In what appears to be the only experimental investigation of the impact of a biocontrol agent on non-target native species in Australia, and one of only a few such studies internationally, Willis *et al.* (1993, 1995, 1998, in press) demonstrated that, although *H. gramineum* is commonly colonised by *Aculus hyperici*, the agent does not significantly impact on the native's growth or reproductive potential, even when plants are environmentally stressed. Moreover, infestation by *A. hyperici* does not hamper the native's ability to recover from drought, whereas it reduces the weed's ability to do so (Willis *et al.*, in press).

Willis *et al*. (1993) maintained *Aphis chloris* on *H. gramineum* experimentally in the glasshouse, but found no significant impact of the agent on the native, despite causing significant reductions in some measures of the target weed's performance. *A. chloris* has never been observed on *H. gramineum* in the field, despite many hours of searching (Willis, unpublished). Based on the results of the glasshouse study (Willis *et al.*, 1993), which was conducted under conditions to optimise potential effects of the agent, it seems unlikely that *A. chloris* would affect any measure of *H. gramineum*'s growth if the native were to be colonised by this agent.

In contrast to the impacts of *A. chloris*, *C. quadrigemina* adults were observed attacking *H. gramineum* plants growing within about 50 m of a heavily attacked population of St. John's wort (Willis, unpublished). Unfortunately, the impact of *C. quadrigemina* on *H. gramineum* was not documented. However, the impact is likely to have been severe, as each attacked individual of the small (< 30 cm high) herbaceous native, hosted about 10-20 adult beetles. In seasons when *C. quadrigemina* is abundant and damaging on St. John's wort, significant impacts on adjacent populations of *H. gramineum* are likely, but the sporadic impacts and associated efficacy of *C. quadrigemina* controlling St. John's wort in Australia, is also likely to limit any sustained damage to *H. gramineum*, particularly as the native is so widespread (Auld & Medd, 1987).

While the broad geographic distribution of St. John's wort and *H. japonicum* may overlap, potentially providing opportunities for *A. hyperici*, *A. chloris* and *C. quadrigemina* to colonise the latter, *H. japonicum* is more common in damper areas than St. John's wort, and has not been found in direct association with it (Willis, unpublished; CSIRO, 1991), which limits the potential for this native to be attacked.

(6) *Mimosa pigra* (mimosa, giant sensitive plant: Mimosaceae)

Mimosa pigra is a perennial prickly shrub that is native to tropical America. In Australia, the species occurs over 800 km^2 of coastal plains in the Northern Territory, but models of the weed's potential distribution suggest much of tropical Australia may be threatened with invasion (Heard & Forno, 1996).

Since 1983, 10 biocontrol agents have been released in Australia against mimosa, eight of which are known to have established (Julien & Griffiths, 1998). During quarantine-based testing, it was demonstrated that two of these agents, *Neurostrota gunniella* (Davis *et al*., 1991) and *Coelocephalapion pigrae* (Heard & Forno, 1996) were capable of feeding and reproducing on the Australian species, *Neptunia dimorphantha*, *N. gracilis*, *N. major* and *N. monosperma*. Permission to release these agents was granted despite expectations that they might occasionally attack Australian species of *Neptunia*, because the impact of any such attack was expected to be insignificant.

N. dimorphantha (the native species with the highest potential to support development of the agents during quarantine tests) and *N. monosperma* are not likely to be colonised by the biocontrol agents because they occur in open grassland habitats of northern and eastern Australia where the target weed does not occur (Davis *et al.*, 1991).

By contrast, the distributions of both *N. major* and *N. gracilis* are sympatric with *M. pigra* in parts of the Northern Territory. Indeed, *N. major* grows around the fringes of *M. pigra* thickets on the Adelaide river plains (Wilson & Forno, 1995) and, in such areas, *Neurostrota gunniella* is known to attack the native (Forno *et al.*, 2000), as predicted by the quarantine tests. Clearly, the potential for agents to impact adversely on these non-target species, particularly *N. major*, is high, especially as their annual life-cycle (Wheeler *et al.*, 1992) is similar to that of the target weed (Parsons & Cuthbertson, 1992). Nevertheless, any such impacts are expected to be minimal, given the poor performances by agents on the natives during host-testing (Davis *et al.*, 1991; Heard & Forno, 1996). We consider that the risk to native *Neptunia* species is high.

(7) *Rubus fruticosus* (blackberry: Rosaceae)

Rubus fruticosus is an aggregate of at least eight closely related species from Europe, grouped under one name because of difficulties in distinguishing the individual taxa (Parsons & Cuthbertson, 1992). Ongoing research aims to clarify the complex taxonomy of Australian Blackberries, with the intention of improving the biological control of this weedy group (Evans *et al.*, 1998). Blackberries are serious environmental weeds of high rainfall areas, particularly in parts of WA, NSW, Victoria and Tasmania, though they are distributed across most of temperate Australia.

The rust fungus, *Phragmidium violaceum* was studied in Europe between 1978 and 1983 as a potential biological control agent for blackberry. Submissions were being prepared seeking approval to introduce the rust to Australia to help control blackberry, when the rust was identified as already being present in southern Victoria following a deliberate, but illegal introduction in 1984 (Marks *et al.*, 1984). Subsequently, a second strain of the same rust species was introduced legally (Bruzzese & Hasan, 1986a).

Although the virulence of the legal and illegal *Phragmidium* strains differs (Bruzzese, 1995), both are able to infect and reproduce on two Australian species, *Rubus gunnianus* and *R. moorei*. Based on laboratory tests to optimise the germination of rust spores and their subsequent infection of host plants, Bruzzese & Hasan (1986b) observed that the two native species, could be damaged by the rust, although disease severity on the latter was relatively poor (see below). To date, there have been no field studies to document the extent, if any, of damage to non-target native *Rubus* species caused by the rust (D. McLaren, pers. comm.).

Both *Rubus gunnianus* and *R. moorei* are likely to occur in the broad geographic regions in which blackberry occurs. Therefore, documenting the impact of *P. violaceum* on the limited field populations of *R. gunnianus*, in particular, is a priority. That the rust can cause significant reductions in the growth of certain members of the *R. fruticosus* aggregate (Mahr & Bruzzese, 1998) highlights the urgency of studying its impact on *R. gunnianus*, as this native is much smaller and less robust than the target weed (Kirkpatrick, 1997). Nevertheless, *R. gunnianus* is endemic to the alpine and subalpine areas of Tasmania (Kirkpatrick, 1997). Climatically, these are areas in which the germination of *P. violaceum* spores and damaging levels of infection are unlikely, since the average temperature for damaging epidemics of the rust is about 20° C (K. Evans, Tasmanian Institute of Agricultural Research, pers. comm.). Evidently, this aspect of the agent's biology is likely to limit significant impacts on *R. gunnianus*. Climatic requirements for epidemics of the illegal rust are relatively poorly understood. Its potential to infect *R. gunnianus* may, therefore, be relatively high and clearly requires further investigation in this regard.

While climatic conditions more conducive to epidemics of *P. violaceum* occur in the region in which *R. moorei* is indigenous, Bruzzese & Hasan (1986a) classified *R. moorei* as 'resistant' to *P. violaceum* under optimal laboratory conditions for germination of rust spores. Any infection of *R. moorei* by *P. violaceum* is, therefore, unlikely to be damaging.

Research into alternative strains of *P. violaceum* that may control relatively resistant taxa within the *R. fruticosus* aggregate is continuing (K. Evans, Tasmanian Institute of Agricultural Research, pers. comm.), and will include testing the potential for these new rust strains to infect and damage key native species, including *R. gunnianus* and *R. moorei* (L. Morin, CSIRO Entomology, pers. comm.).

(8) *Rumex pulcher* (fiddledock: Polygonaceae)

Rumex is a world-wide genus including several weedy species that have been targeted for biological control (Julien & Griffiths, 1998; Scott, 1990). The genus is divided into four subgenera. The subgenus *Rumex* includes *R. pulcher* (Rechinger, 1984), and four other proclaimed weeds (Parsons & Cuthbertson, 1992).

Rumex pulcher is distributed across warm-temperate southern Australia on a range of moist soil-types. Although mature plants are problematic because they exclude more favourable species, and high densities of their dried seed stems hinder grazing, more juvenile plants with rosettes can be valuable for grazing at times when other fresh food is limited (McGhie *et al.*, 1983). The biocontrol program against *R. pulcher* therefore aims to decrease the vigour of larger plants, by targeting agents that attack the weed's vigorous root system (Scott & Sagliocco, 1991a).

Herbarium records highlight the potential for each of the eight Australian *Rumex* species (Rechinger, 1984) to co-occur with fiddledock. This is noteworthy given the clear potential for *Synansphecia doryliformis* - the only agent released against fiddledock to date - to attack and damage native *Rumex* species (Scott & Sagliocco, 1991a). Although approval was granted to release a second agent, *Bembecia chrysidiformis* (Lepidoptera: Sessiidae; Scott & Sagliocco, 1991b), it had not been released by 1996 (Julien & Griffiths, 1998). In the case of S. *doryliformis*, approval to release the moth is noteworthy, given that damage to some native *Rumex* species was possible (Scott & Sagliocco, 1991a), largely because the agent appears able to utilise most species within the subgenus *Rumex* as host plants (Scott, 1990; Scott & Sagliocco, 1991a).

While acknowledging that some of the Australian *Rumex* species may be attacked by *S. doryliformis*, Scott (1990) outlined reasons to expect that potential impacts on native species would be acceptable and/or likely to be limited. Regarding *R. brownii*, *R. crystallinus*, *R. dumosus* and *R. bidens*, Scott (1990) observed that these natives have themselves been considered weedy, at least locally (Allen, 1974), thereby implying that if they were to be damaged by either of the *R. pulcher* agents, that the damage would be acceptable. Scott (1990) also observed that significant impacts on *R. bidens* were unlikely, because this species is semi-aquatic (Rechinger, 1984), a habitat to which the biocontrol agents are not adapted.

Host plant ecology is also likely to limit potential sustained impacts on *R. crystallinus* and *R. tenax.* The former is an annual, upon which neither *S. doryliformis* nor *B. chrysidiformis* could complete larval development (Scott, 1990) and both species are geographically isolated from the target weed, occurring in the drier central regions of Australia outside the climatic range of the agents (Scott, 1990).

The remaining threatened natives comprise *R. stenoglottis*, *R. alcockii* and *R. drummondii.* There are no clear ecological or geographical barriers to prevent colonisation of these natives by the biocontrol agents for *R. pulcher*, but their relatively low abundance and restricted distribution may limit the likelihood of being colonised. Scott (1990) and Scott & Sagliocco (1991a) make the general observation that, as with the target weeds, the survival of individual native plants is unlikely to be endangered by the herbivores, because they attack only mature plants that have already reproduced. Nevertheless, it is clear that, in the longer term, these impacts on individual plants may have detrimental consequences for populations of the natives. This expectation underscores Scott's (1990) observation, prior to the agents' release, that the Australian authorities need to accept that the benefits of controlling the weed outweigh the risks to native *Rumex* species.

We have assessed that *S. doryliformis* poses a low risk to *R. bidens*, a moderate risk to *R. brownii*, *R. crystallinus*, *R. dumosus* and *R. tenax*, and a moderate-high risk to *R. alcockii*, *R. drummondii* and *R. stenoglottis*.

(9) *Senecio jacobaea* (ragwort: Asteraceae)

This herbaceous species was introduced to Australia in the mid-late 1800s and quickly spread to become a weed of cleared land and pasture, particularly in Victoria and Tasmania. The weed has potential to co-occur with many related Australian congenerics. Of particular interest, however, is its broad geographical sympatry with *S. lautus*, *S. glomeratus*, *S. linearifolius* and *S. quadridentatus*. During host-testing, each of these native species supported low levels of feeding and reproduction by two of the five biocontrol agents for ragwort that have been released in Australia, (*Cochylis atricapitana* and *Longitarsus flavicornis*; J. Cullen, unpublished), while two more are assumed to do so (*L. jacobaeae* and *Tyria jacobaeae*). Other Australian native *Senecio* species may also be threatened by the ragwort agents. Certainly, *T. jacobaeae* is known to colonise and adversely impact on at least one North American non-target *Senecio* species, *S. triangularis* (Diehl & McEvoy, 1990). Significantly, however, agent behaviour, climate and habitat preferences appear to limit the rate at which *T. jacobaeae* attacks, and subsequently damages, *S. triangularis* (Diehl & McEvoy, 1990; Harris & McEvoy, 1995).

Based on the distribution of some potential Australian non-targets including *S. lautus*, *S. glomeratus*, *S. linearifolius* and *S. quadridentatus*, there is a clear possibility that the ragwort biocontrol agents may attack these Australian species. However, if the attacks were to occur it seems unlikely that they would cause any significant damage, either due to difficulties in establishing the agent on the target weed (Julien & Griffiths, 1998) or to the very low level of attack observerd in testing.

Despite multiple introductions of *Tyria jacobaeae*, its poor establishment probably reflects high levels of larval predation (Ireson & Holloway, 1999). Indeed, with the exception of one site in southern Victoria (R. Kwong, pers. comm.), *T. jacobaeae* does not appear to have established on the Australian mainland. Under these circumstances, impacts on non-target hosts that would be of poor quality compared to the target weed are likely to be minor.

Morphological and ecological characteristics of the threatened *Senecio* species may also limit damage to these plants, if they are attacked. For example, the lack of a distinct rosette and fleshy rootstock in the native species limits their attractiveness for oviposition by the *Longitarsus* spp. and for development of the larvae of these species and *C. atricapitana*. Moreover, each of the threatened native species is widespread and locally abundant, to the extent that some of them have also been considered weedy in some areas (Auld & Medd, 1987).

Although we were unable to locate published information on the host-tests for the ragwort agents, taken together, the information that we present suggests that the threats posed to *S. lautus*, *S. glomeratus*, *S. linearifolius* and *S. quadridentatus* by *Cochylis atricapitana*, *Longitarsus flavicornis*, *L jacobaeae* and *Tyria jacobaeae* are very low.

Limitations of the study

The primary objective of this study was to determine the native plant species that are at the greatest risk of being utilised as alternative hosts by biocontrol agents introduced against major introduced weed species. After collating the information necessary to highlight such threatened native species, we also evaluated the threat posed by the agent(s) to the native(s), based on the available information. The study was limited by both the availability of published data and access to formal host-specificity records that are archived within several government agencies. As with Pemberton (2000), we relied, therefore, on the experience of biocontrol practitioners to point out relevant potential 'case studies'. Clearly, reliance on the memory and experience of individual practitioners risks subjectivity and potential bias, but in the absence of other sources of information, such a project would not have been possible. If nothing more, our results highlight about 30 native species at varying degrees of endangerment by weed biocontrol agents. Despite clear potential to underestimate the threat, this study is the first of its kind in Australia and one of few internationally (but see Pemberton, 2000), to begin the process of assessing the safety of the discipline of biological weed control.

Another potential limitation of the study is the reliability with which collections of herbarium specimens are able to predict the distribution of plant species. In this regard, our analysis is limited to the current geographical distribution of targeted weed species, but there is clear potential, as in the case, for example, of mimosa (Heard & Forno, 1996), for weed distributions to expand significantly. Were this to happen, the threat posed by biocontrol agents to physiologically suitable, but geographically isolated natives may be increased, because the potential for agents to encounter suitable native hosts may increase commensurately with the expansion of the weed's range. As always, this risk must be balanced against the environmental and agricultural risks of not controlling weeds that are spreading aggressively (Fowler *et al.*, 2000; McFadyen *et al.* 2002; Thomas & Willis, 1998).

While the current distribution of weeds is relatively well understood, either because of their agricultural and environmental impacts and/or because of their sheer abundance, that of the natives may be relatively poorly documented, particularly for cryptic or rare species that may occur in isolated environments. If species' distribution maps underestimate the actual distribution of rare species, the threat posed to them by biocontrol agents may be overestimated. Ironically, it is these cryptic species that may be of greatest interest to environmentalists since their small populations may be particularly vulnerable to biocontrol agents. Moreover, their isolation or rarity means that potential impacts can be difficult to assess.

In fact, sound biocontrol practice can help to locate and conserve rare species. Such was the case for *Rumex drummondii* which was considered to be either extinct, or a synonym for *R. dumosus* (Rechinger, 1984) prior to testing potential agents for *R. pulcher*. To complete specificity tests for *Synansphecia doryliformis* and *Bembecia chrysidiformis* Scott & Yeoh (1995) conducted intensive surveys that led to the rediscovery of *R. drummondii*, which is now recognised formally as a rare Western Australian endemic (Briggs & Leigh, 1996). While it is likely that the isolation of *R. drummondii* limits attack by biocontrol herbivores, its rediscovery by biocontrol practitioners potentially enables detailed monitoring of the species for damage by the agents and, if necessary, its protection from the agents, among more general conservation efforts. In the absence of a biocontrol program for fiddledock, *R. drummondii* may not have been rediscovered and the active conservation of a rare species would not have been possible, irrespective of the biocontrol program for *R. pulcher*.

Further work

(i) Empirical field studies In outlining research needs to improve the environmental safety of biological weed control, Hopper (2000) questions which species should be the focus of empirical research to evaluate the impact of agents on non-targets. What, for example, are the relative advantages and disadvantages of focussing on beneficial, rare or keystone species (Hopper, 2000)?

Pemberton (2000) demonstrates that attack of non-target plant species by weed biocontrol agents is most likely when the non-target is closely related to the weed. Studying a potential agent for *Heliotropium amplexicaule* in Australia, Briese & Walker (2002) reiterate this observation. Our results also suggest that associated with a long history of biological weed control in Australia, the native species that are at greatest risk of attack and potential damage are often in the same genus, and consistently in the same family, as the target weed. As in the case of *Rumex drummondii*, threatened species may include rare, or other considerations, of a species' value. Biological weed control appears to predict successfully the potential physiological host range of agents, especially as it is unlikely that they will evolve to acquire novel, distantly related, hosts (Marohasy, 1996).

Predicting the physiological host range of agents is critical to pre-release assessments of potential attack of non-target species by biocontrol agents and, therefore, whether or not the agent is considered for further testing or field release. With notable exceptions, however (see, for example, Andres, 1985; Diehl & McEvoy, 1990; Louda *et al*., 1997; Turner *et al.*, 1987; Willis *et al.*, 1993, 1995, 1998; Willis *et al.*, in press), evaluating the damage caused to non-target native species by agents does not appear to have been undertaken systematically (Hopper, 2000; Pemberton, 2000), even where field observations indicate that native species are being attacked. Clearly, a thorough examination of the safety of biological weed control in Australia, and elsewhere, urgently requires more empirical, field-based studies. Typically, we expect that these studies will demonstrate that, despite colonisation of natives, the actual impacts on plant or population performance are biologically insignificant. Although insignificant results may be predictable, less exciting than demonstrating significant impacts on the target weed and potentially difficult to publish in peer-reviewed literature (Csada & James, 1996), meaningful reviews of the environmental safety of biological weed control are impossible without them, and the environmental safety of biocontrol will continue to be challenged.

Given the apparent success of biocontrol in predicting the physiological host range of agents (Briese & Walker, 2002; Marohasy, 1996; Pemberton, 2000), we expect that post-release evaluations of impacts on non-target native species will underscore the pre-release predictions of potential attack, as they did in the case of *Aculus hyperici* and *Hypericum gramineum* (Willis *et al.*, 1993, 1995, 1998; in press) and, indeed, in the case of *Rhinocyllus conicus* and North American thistles (Zwölfer & Harris, 1984). Moreover, field evaluations of impacts on realised hosts (cf. potential hosts, as demonstrated in the laboratory) will highlight the role of various ecological, geographical, behavioural, temporal, spatial and/or other considerations in moderating the likelihood of attack. Many of these variables ultimately support decisions to field-release agents that are not monophagous, as outlined for the introductions discussed above. Evaluating the efficacy of these moderating factors is an important component of assessing predictions of agent safety, after their release.

(ii) Indirect effects In this study, we have concentrated on the potential for weed biocontrol agents to attack non-target native species directly. Potentially, however, agents may affect other species in the ecological community indirectly (Fowler *et al.*, 2000; Lonsdale *et al.*, 2000; Strong & Pemberton, 2000), even if the agent itself is highly host-specific. Henneman & Memmott (2001) demonstrated this recently using food webs constructed in an invaded ecological community in Hawaii. Although their study emphasised concerns about the safety of biological control programs for arthropod pests, the same issues relate to biological weed control.

In the context of the potential impacts on the non-target Australian plant species discussed above, there is clear potential for indirect effects on non-target arthropod species which are known to inhabit threatened relatives of, for example, rubber vine (McFadyen *et al.* 2002), St. John's wort (Berentson, 1999) and Paterson's curse (see above reference to native Australian *Dialectica* species). If native plants are attacked by biocontrol agents, quantitative food webs are one tool to investigate such indirect effects and offer a powerful means of examining: the direct impacts of the agent on native plants; their indirect impact(s) on native herbivore abundance, and the potential for both direct and indirect effects to reticulate throughout the food web, with potentially important, but largely unpredicted, consequences. In the same way that the risks of introducing an agent that may attack a native plant must be weighed against the advantages of controlling an invasive weed (Fowler *et al.*, 2000; McFadyen *et al.* 2002; Thomas & Willis, 1998), potential indirect effects, which may be more difficult to predict than direct impacts (Fowler *et al.*, 2000), also must be weighed against the benefits of weed control. Food webs are likely to play an increasingly important role in future assessments of the safety of biological control (Strong & Pemberton, 2000).

Conclusions

Based on assessment of the physiological host range of biological weed control agents, this study highlighted 17 agents that have been released in Australia against 9 weed species, with potential to attack at least 30 species of native plants. In fact, the number of native species that are actually attacked will almost certainly be lower than 30. This is because the geographical distribution of targeted weeds and relevant threatened natives combine with various ecological aspects of the agent and/or potential native hosts to limit the probability of agents encountering all physiologically suitable natives. The number of agents that adversely affect natives will be lower still (and may, indeed, be zero). However, without empirical field evaluations addressing this aspect of biological weed control, it is difficult to draw this conclusion with certainty.

The case of *Aculus hyperici* appears to be the only published evaluation of potential damage to non-target native species in Australia. The *Aculus* case demonstrated the accuracy of predictions that *H. gramineum* would be attacked, but that the associated impacts would be minimal. A high priority for further work is to evaluate the impact of other threatening biocontrol agents on the native species that are most likely to be attacked. Our data suggest that evaluating the impacts of four biocontrol agents on key native species, as summarised below, is particularly urgent:

- *Euclasta gigantalis*, released against rubber vine, on *Gymnanthera oblonga*;
- *Neurostrota gunniella*, released against mimosa, on *Neptunia major*;
- *Phragmidium violaceum* (particularly the 'illegal strain'), released against blackberry, on *Rubus gunnianus*; and
- *Synansphecia doryliformis* and, potentially, *Bembecia chrysidiformis*, released against fiddledock, on *Rumex drummondii*.

The urgency of evaluating the first two cases reflects field observations that native species were attacked by *E. gigantalis* and *N. gunniella* when the natives were closely associated with populations of the target weed that were also attacked. The urgency of evaluating the impact of *Phragmidium violaceum* highlights expectations that *R. gunnianus* is likely to be infected by the rust and that although the legal strain is unlikely to impact significantly on the native, *R. gunnianus*, considerably less is known about the climatic requirements for epidemic development of the illegal strain. Finally, the urgency of evaluating impacts of the fiddledock agents on *R. drummondii* reflect its rarity, an absence of clear physical or biological barriers to attack, and evidence that the native co-occurs with weedy relatives that themselves, may be colonised by the agents. As Louda *et al.* (1997) and others (e.g. Turner *et al.*, 1987) acknowledge, impacts of biocontrol agents on rare or endangered native species are particularly concerning. Were they to occur at significant levels, such impacts would cause considerable harm to the comparatively safe image of biological weed control.

With the possible exception of the fiddledock agents on *R. drummondii,* about which we have limited information, our expectation is that evaluation of the above impacts will confirm that populations of threatened natives are not being affected adversely by biocontrol agents. To this extent, we expect that laboratory predictions of agent safety will be realised and anticipate that the risk posed by the agents to native biodiversity will have been acceptable. This expectation assumes, to some extent, that the agents contributed to reductions in the weeds' severity. In the future, we expect that demonstrating the environmental safety of agents after their release will be as important to weed biocontrol as documenting the successful management of the targeted weed.

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References

Allen, J.M. (1974) Preliminary observations and investigations on docks (*Rumex* spp.) in Western Australia. *Western Australian Department Agriculture Technical Bulletin,* **23**, 1-5.

Andres, L.A. (1985) Interaction of *Chrysolina quadrigemina* and *Hypericum* spp. in California. *Proceedings of the VI International Symposium on the Biological Control of Weeds, Vancouver, Canada, 1984* (ed E.S. Delfosse), pp. 235-239. Agriculture Canada, Ottawa.

Auld, B.A. & Medd, R.W. (1987) *Weeds: An Illustrated Botanical Guide to the Weeds of Australia* Inkata Press Pty Ltd, Melbourne.

Berentson, P.R. (1999) *The Impact of a Biocontrol Mite on a Target Weed and Non-target Native Plants* Honours Thesis, The Australian National University, Canberra.

Briese, D.T. (1989) Host-specificity and virus-vector potential of *Aphis chloris* (Hemiptera: Aphididae), a biological control agent for St. John's Wort in Australia. *Entomophaga*, **34**, 247-264.

Briese, D.T. & Walker, A. (2002) A new perspective on the selection of test plants for evaluating the host-specificity of weed biological control agents: the case of *Deuterocampta quadrijuga*, a potential insect control agent of *Heliotropium amplexicaule*. Biological Control 25, 273-287.

Briggs, J.D. & Leigh, J.H. (1996) *Rare or Threatened Australian Plants* CSIRO Publishing, Collingwood.

Bruzzese, E. (1995) Present status of biological control of European blackberry (*Rubus fruticosus* aggregate) in Australia. *Biological Control of Weeds: Proceedings of the VIII International Symposium on Biological Control of Weeds, Lincoln University, Canterbury, New Zealand, 1992* (eds E.S. Delfosse & R.R. Scott), pp. 297-299. DSIR/CSIRO, Melbourne.

Bruzzese, E. & Hasan, S. (1986a) Host specificity of the rust *Phragmidium violaceum*, a potential biological control agent of European blackberry. *Annals of Applied Biology,* **108**, 585-596.

Bruzzese, E. & Hasan, S. (1986b) Infection of Australian and New Zealand *Rubus* subgenera *Dalibarda* and *Lampobatus* by the European blackberry rust fungus *Phragmidium violaceum*. *Plant Pathology,* **35**, 413-416.

Csada, R.D. & James, P.C. (1996) The "file drawer problem" of non-significant results: does it apply to biological research? *Oikos*, **76**, 591-593.

CSIRO (1991) *The Host-specificity of Aculus hyperici (Liro) (Acarina: Eriophyidae) in Relation to Different Species in the Genus* Hypericum. CSIRO Entomology Application to the Australian Plant Quarantine and Inspection Service, Canberra, Australia.

Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. & Leigh, J.H. (1981) *Plants of western New South Wales* NSW Government Printing Office and Soil Conservation Service of NSW, Sydney.

Davis, D.R., Kassulke, R.C., Harley, K.L. & Gillett, J.D. (1991) Systematics, morphology, biology, and host specificity of *Neurotrostrota gunniella* (Busck) (Lepidoptera: Gracillariidae), an agent for the biological control of *Mimosa pigra L. Proceedings of the Entomological Society of Washington*, **93**, 16-44.

Diehl, J. & McEvoy, P. (1990). Impact of the cinnabar moth (*Tyria jacobaeae*) on *Senecio triangularis*, a non-target native plant in Oregon. *Proceedings VII International Symposium on Biological Control of Weeds, 6-11 March 1988, Rome, Italy* (ed E.S. Delfosse),pp. 119-126. Ministero dell'Agricoltura e delle Foreste/ CSIRO, Melbourne.

Evans, K.J., Symons, D.E. & Roush, R.T. (1998) Taxonomy and genotypes of the *Rubus fruticosus* L. aggregate in Australia. *Plant Protection Quarterly*, **13**, 152-156.

Forno, I.W., Fichera, J. & Prior, S. (2000) Assessing the risk to *Neptunia oleracea* Lour. by the moth, *Neurostrota gunniella* (Busck), a biological control agent for *Mimosa pigra L. Proceedings of the X International Symposium on Biological Control of Weeds, Bozeman, Montana, USA, 1999* (ed N.R. Spencer), pp. 449-457. Montana State University, Bozeman, USA.

Fowler, S.V., Syrett, P. & Hill, R.L. (2000) Success and safety in the biological control of environmental weeds in New Zealand. *Austral Ecology*, **25**, 553-562.

Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281-290.

Harris, P. & McEvoy, P. (1995) The predictability of insect host plant utilisation from feeding tests and suggested improvements for screening weed biological control. *Biological Control of Weeds: Proceedings of the VIII International Symposium on Biological Control of Weeds, Lincoln University, Canterbury, New Zealand, 1992* (eds E.S. Delfosse & R.R. Scott), pp. 125-131. DSIR/CSIRO, Melbourne.

Hasan, S. & Delfosse, E.S. (1995) Susceptibility of the Australian native, *Heliotropium crispatum*, to the rust fungus *Uromyces heliotropii* introduced to control common heliotrope, *Heliotropium europaeum. Biocontrol Science and Technology*, **5**, 165-174.

Hasan, S., Delfosse, E.S., Aracil, E. & Lewis, R.C. (1992) Host-specificity of *Uromyces heliotropii*, a fungal agent for the biological control of common heliotrope (*Heliotropium europaeum*) in Australia. *Annals of Applied Biology*, **121**, 697-705.

Heard, T.A. & Forno, I.W. (1996) Host selection and hosts range of the flower-feeding weevil, *Coelocephalapion pigrae*, a potential biological control agent of *Mimosa pigra. Biological Control*, **6**, 83-95.

Henneman, M.L. & Memmott, J. (2001) Infiltration of a Hawaiian community by introduced biological control agents. *Science*, **293**, 1314-1316.

Hopper, K.R. (2000) Research needs concerning non-target impacts of biological control introductions. *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp. 39-56. CABI Publishing, Wallingford.

Ireson, J.E. & Holloway, R.J. (1999) An overview of the establishment, distribution and efficacy of biological control agents for ragwort, *Senecio jacobaea L.*, in Tasmania. *12th Australian Weeds Conference: Papers & Proceedings, 12-16 September 1999, Hobart, Tasmania* (eds A.C. Bishop, M. Boersma & C.D. Barnes), pp. 425-430. Tasmanian Weed Society, Hobart.

Jessop, J.P. & Toelken, H.R., eds. (1986) *Flora of South Australia part 3: Polemoniaceae - Compositae*. South Australian Government Printing Division, Adelaide.

Johnson, D.M. & Stiling, P. (1996) Host-specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. *Environmental Entomology,* **25**, 743-748.

Johnson, D.M. & Stiling, P. (1998) Distribution and dispersal of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia* feeding moth, in Florida. *Florida Entomologist*, **81**, 12-22.

Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds*, 4th edn. CABI Publishing, Wallingford, UK.

Julien, M.H., Griffiths, M.W. & Stanley, J.N. (2001) *Biological Control of Water Hyacinth 2: the Moths* Niphograpta albiguttalis *and* Xubida infusellus: *Biologies, Host Ranges, and Rearing, Releasing and Monitoring Techniques for Biological Control of* Eichhornia crassipes ACIAR, Canberra.

Kirk, A.A. & Wapshere, A.J. (1979) The life history and host specificity of the *Echium* borer, *Phytoecia coerulescens* [Col.: Cerambycidae]. *Entomophaga,* **24**, 423-430.

Kirkpatrick, J. (1997) *Alpine Tasmania: an Illustrated Guide to the Flora and Vegetation* Oxford University Press, Melbourne.

Lonsdale, W.M., Briese, D.T. & Cullen, J.M. (2000) Risk analysis and weed biological control. *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp. 185-210. CABI Publishing, Wallingford.

Louda, S.M. (1998) Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. *Environmental Entomology*, **27**, 834-841.

Louda, S.M., Kendall, D., Connor, J. & Simberloff, D. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science*, **277**, 1088-1090.

Mahr, F.A. & Bruzzese, E. (1998) The effect of *Phragmidium violaceum* (Shultz) Winter (Uredinales) on *Rubus fruticosus* L. agg. in south eastern Victoria. *Plant Protection Quarterly*, **13**, 182-186.

Marks, G.C., Pascoe, I.G. & Bruzzese, E. (1984) First record of *Phragmidium violaceum* on blackberry in Victoria. *Australasian Plant Pathology*, **13**, 12-13.

Marohasy, J. (1996) Host shifts in biological weed control: real problems, semantic difficulties or poor science? *International Journal of Pest Management*, **42**, 71-75.

McFadyen, R.E.C., Vitelli, M. & Setter, C. (2002) Host specificity of the Rubber vine moth *Euclasta whalleyi* Popescu-Gorj & Constantinescu (Lepidoptera:Crambidae: Pyraustinae): field host range compared to the predicted by laboratory tests. *Australian Journal of Entomology*, **41**, 321-323.

McFadyen, R.E.C. & Marohasy, J.J. (1990) A leaf feeding moth, *Euclasta whalleyi* [Lep.: Pyralidae] for the biological control of *Cryptostegia grandiflora* [Asclepiadaceae] in Queensland, Australia. *Entomophaga*, **35**, 431-435.

McGhie, D.A., Sprivulis, R., Dixon, F.F., Sawyer, G.J., McMullen, G. & Silcock, J. (1983) Dock - weed or pasture plant? *Western Australian Department Agriculture Journal of Agriculture*, **24**, 87-89.

Mo, J., Trevino, M. & Palmer, W.A. (2000) Establishment and distribution of the rubbervine moth *Euclasta whalleyi* Popescu-Gorj & Constantinescu (Lepidoptera: Pyralidae) following its release in Australia. *Australian Journal of Entomology*, **39**, 344-350.

Parsons, W.T. & Cuthbertson, E.G. (1992) *Noxious Weeds of Australia* Inkata Press, Melbourne.

Pemberton, R.W. (2000) Predictable risk to native plants in weed biological control. *Oecologia*, **125**, 489-494.

Rechinger, K.H. (1984) *Rumex* (Polygonaceae) in Australia: a reconsideration. *Nuytsia*, **5**, 75-122.

Scott, J.K. (1990) Prospects for the biological control of Rumex species in Australia. *Proceedings VII International Symposium on Biological Control of Weeds, 6-11 March 1988, Rome, Italy* (ed E.S. Delfosse), pp. 425-428. Ministero dell'Agricoltura e delle Foreste/CSIRO, Melbourne.

Scott, J.K. & Sagliocco, J.-L. (1991a) *Chamaesphecia doryliformis* (Lep.: Sessiidae), a second root borer for the control of *Rumex* spp. (Polygonaceae) in Australia. *Entomophaga*, **36**, 245-251.

Scott, J.K. & Sagliocco, J.-L. (1991b) Host-specificity of a root borer, *Bembecia chrysidiformis* (Lep.: Sessiidae), a potential control agent for *Rumex* spp. (Polygonaceae) in Australia. *Entomophaga*, **36**, 235-244.

Scott, J.K. & Yeoh, P.B. (1995) The rediscovery and distribution of *Rumex drummondii* (Polygonaceae) in south-western Australia. *Australian Journal of Botany*, **43**, 397-405.

Sheppard, A.W. (1996) The interaction between natural enemies and interspecific plant competition in the control of invasive pasture weeds. *Proceedings of the IX International Symposium on Biological Control of Weeds, Stellenbosch, South Africa, 1996* (eds V.C. Moran & J.H. Hoffmann), pp. 47-53. University of Cape Town, Cape Town.

Sheppard, A.W., Smyth, M.J. & Swirepik, A. (2001) The impact of a root-crown weevil and pasture competition on the winter annual *Echium plantagineum. Journal of Applied Ecology*, **38**, 291-300.

Simberloff, D. & Stiling, P. (1996a) How risky is biological control? *Ecology*, **77**, 1965-1974.

Simberloff, D. & Stiling, P. (1996b) Risks of species introduced for biological control. *Biological Conservation*, **78**, 185-192.

Strong, D.R. & Pemberton, R.W. (2000) Food webs, risks of alien enemies and reform of biological control. *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp. 57-79. CABI Publishing, Wallingford.

Thomas, M.B. & Willis, A.J. (1998) Biocontrol - risky but necessary? *Trends in Ecology and Evolution*, **13**, 325-329.

Turner, C.E. (1985) Conflicting interests and biological control of weeds. *Proceedings of the VI International Symposium on the Biological Control of Weeds, Vancouver, Canada, 1984* (ed E.S. Delfosse), pp. 203-225. Agriculture Canada, Ottawa.

Turner, C.E., Pemberton, R.W. & Rosenthal, S.S. (1987) Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. *Environmental Entomology*, **16**, 111-15.

Wapshere, A.J. & Kirk, A.A. (1977) The biology and host specificity of the *Echium* leaf miner *Dialectica scallariella* (Zeller) (Lepidoptera: Gracillariidae). *Bulletin of Entomological Research,* **67**, 627-633.

Wheeler, J.R., Rye, B.L., Koch, B.L. & Wilson, A.J.G. (1992) *Flora of the Kimberley region* Western Australian Herbarium and Department of Conservation and Land Management, Como, WA.

Willis, A.J., Ash, J.E. & Groves, R.H. (1993) Combined effects of two arthropod herbivores and water stress on growth of *Hypericum* species. *Oecologia*, **96**, 517-525.

Willis, A.J., Ash, J.E. & Groves, R.H. (1995) The effects of herbivory by a mite, *Aculus hyperici*, and nutrient deficiency on growth in *Hypericum* species. *Australian Journal of Botany*, **43**, 305-316.

Willis, A.J., Ash, J.E. & Groves, R.H. (1998) Interactions between plant competition and herbivory on the growth of *Hypericum* species: a comparison of glasshouse and field results. *Australian Journal of Botany*, **46**, 707-721.

Willis, A.J., Berentson, P.R. & Ash, J.E. (2003) Impacts of a weed biological control agent on recovery from water stress in a target and a non-target *Hypericum* species. *Journal of Applied Ecology*, **40**, in press.

Wilson, C.G. & Forno, I.W. (1995) The biological control programme against *Mimosa pigra* in Australia's Northern Territory. *Biological Control of Weeds: Proceedings of the VIII International Symposium on Biological Control of Weeds, Lincoln University, Canterbury, New Zealand, 1992* (eds E.S. Delfosse & R.R. Scott), pp. 75-80. DSIR/CSIRO, Melbourne.

Zwölfer, H. & Harris, P. (1984) Biology and host specificity of *Rhinocyllus conicus* (Froel.) (Col., Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans L. Zeitschrift fur Angewandte Entomologie*, **97**, 36-62.

Evaluating the effectiveness of weed biocontrol at the local scale

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Summary

Too many biocontrol programs have focused mainly on the establishment and prevalence of the biocontrol agents, with only limited studies on the impact of biocontrol at the individual plant level. Long-term effectiveness of biocontrol at the population level of the weed, and the resulting social and economic benefits are often not studied. The need for a comprehensive evaluation as an integral part of any biocontrol program, reasons for the limited emphasis on evaluation studies, and the potential role of community organizations in evaluation studies are discussed. Advantages and disadvantages of various evaluation methods such as before and after release assessments, simulation experiments, relating damage levels to plant performance, and exclusion methods are compared. Evaluation methods commonly used in weed biocontrol programs in Australia are highlighted, along with an assessment on the success rates achieved. Evaluation protocols for aquatic and terrestrial weeds are suggested.

Key words: biocontrol, evaluation, methods, local scale

Introduction

Weed biocontrol programs have focused mainly on the establishment and prevalence of the biocontrol agents, with only limited studies on the impact of biocontrol at the weed population level (Hoffmann & Moran, 1998; McClay, 1995; McEvoy *et al.*, 1991). In Australia, more than 40% of weed biocontrol programs have had no negative impact on target weeds (Briese, 2000a). But the long-term impact of biocontrol, and the resulting social and economic benefits, impact on non-target organisms, and end-user satisfaction are often not studied. This is because evaluation is expensive, and requires long-term funding commitments and community support. Evaluation is also often perceived as basic research with no additional benefits to the community and the funding agencies, and is not a politically sensitive issue (McFadyen, 2000). However, evaluation is essential to:

- Measure the success or failure of biocontrol
- Satisfy government and funding bodies
- Increase the profile of biocontrol
- Extrapolate results to a regional scale
- Attract funding for future research
- Provide a sense of satisfaction and achievement

In this review a more generic model for evaluation at the local scale is presented along with suggested protocols. For details on the evaluation process and methodology for individual weeds, readers are referred to the following reviews: Auld, 2000; Briese, 2000a; Forno & Julien, 2000; and Syrett *et al.*, 2000.

Evaluation at a local scale

The success or failure of a biocontrol program can be measured by quantifying the populations of the biocontrol agents and their target weeds, and the resulting economic and social benefits. However, for environmental weeds it is often difficult to quantify either economic or social values. Evaluation at a local scale involves the following measurements:

- Prevalence and abundance of biocontrol agents over space and time
- Impact of biocontrol at individual plant and weed population levels.
- Assessment of system responses such as increase in pasture production, reduction in health hazards, increases in native plant species diversity, etc.
- Long-term impact of biocontrol on the target weed and other non-target organisms.

Evaluation methods

The success of a biocontrol program depends on the establishment of the biocontrol agent, and hence evaluation should initially focus on the agent establishment on a spatial scale. This could be obtained either by direct survey or through feedback from end-users. Abundance of biocontrol agents does not necessarily result in weed control. Hence, it is essential to quantify the impact of the biocontrol agents on the target weeds. Before and after-release assessments, simulation experiments either in the glasshouse or in the field, relating plant performance to damage levels by the biocontrol agents, biocontrol exclusion methods, and monitoring the long-term changes in target weed populations are the common evaluation methods.

Difficulties in evaluation

Evaluation is labour intensive and involves both extensive (spatial and time scale) and intensive (individual plant and weed population levels) studies. Different evaluation methods may be required for different weeds, but all methods have deficiencies. Evaluation both at a local and regional scale often requires community support, and is dependent on local weather conditions, often resulting in erratic (but realistic) results. Timing of the evaluation is also an important factor, and evaluations conducted too early before agents have had a chance to achieve their full potential could give misleading results (McFadyen, 1998).

Visual impressions

This is a relatively simple method to demonstrate the impact of biocontrol agents. Before-and-after release photographs demonstrating the success of biocontrol of *Opuntia stricta*, *Eichhornia crassipes* and *Salvinia molesta* in Queensland are the best examples. This method is more reliable for weeds where the biocontrol agents have become abundant and cause drastic reductions in the target weeds within a short period. However, such dramatic changes in target weed populations often do not occur. In some circumstances, the agent may take several years to become abundant. In weeds with multiple agent introductions, variable and prolonged establishment times for different agents make the “before-and-after” release comparisons less reliable without adequate quantitative data. In the case of *Parthenium hysterophorus* with 12 biocontrol agents introduced in the last two decades, the time taken for the agents to become abundant ranged from a couple of years (stem galling moth *Epiblema strenunana* Walker, stem boring weevil *Listronotus setosipennis* Hustache and summer rust *Puccinia melampodii* Diet & Holway) to more than a decade (leaf feeding beetle *Zygogramma bicolorata* Pallister and seed feeding weevil *Smicronyx lutulentus* Dietz). Comparisons of photographs of parthenium infestations before and after the outbreak of defoliation by *Z. bicolorata* reveal a general declining trend in weed density (Figure 1). Even though it is highly likely that biocontrol is responsible for the changes in weed density there are no adequate pre-release quantitative data to support this. In other cases, the changes in weed density may be due to reasons other than the biocontrol. Hence, it is essential to get quantitative data to support any “before-and-after” release photographs. For bellyache bush (*Jatropha gossypiifolia*) and sicklepod (*Senna obtusifolia*), Queensland Department of Natural Resources & Mines (QDNR&M) initiated collection of pre-release baseline ecological data well before work on biocontrol was initiated.

Figure 1. Visual impression of the impact of defoliation by the leaf-feeding beetle *Z. bicolorata* on parthenium at Mt Panorama in Central Queensland. November 1996: parthenium infestation before the outbreak of *Z. bicolorata*. January 1997: complete defoliation by *Z. bicolorata*. July 1998: reduced weed density and increased pasture production following the defoliation.

Simulation experiments

This is the simplest of all evaluation methods that can be completed within a short period under controlled conditions. Simulation experiments in the glasshouse and field cage provide valuable information on the potential impact of the biocontrol agents, but often at individual plant level. Such simulation studies provide valuable benchmark information for future field evaluations. In the glasshouse, defoliation for a minimum of 74 days is required to prevent *P. hysterophorus* from producing any seeds (Dhileepan *et al.*, 2000a). Evaluations in the field later proved that biocontrol was effective only in the years when the leaf-feeding *Z. bicolorata* was active for more than three months (Dhileepan, unpublished data). However the results from simulation studies have limited value, as they do not always reflect the impact observed in the field. This is possibly due to the exclusion of other biotic (inter- and intra-specific competition in plants and biocontrol agents, as well as natural enemies of biocontrol agents) and abiotic factors. For example, in simulation experiments, more than four *L. setosipennis* larvae per plant are required to have any negative impact on *P. hysterophorus* (Dhileepan, 2003). But in the field in only 16% of the sites the population of *L. setosipennis* exceeded the threshold level (Dhileepan, 2003). Reznik (2000) also failed to predict the broader-scale performance of the ragweed leaf beetle *Zygogramma saturalis* F. on the basis of simulation and cage experiments. Hence, extrapolating data from simulation experiments to a regional scale should be done with caution.

Damage levels vs. plant performance

Relating damage levels of various biocontrol agents to plant performance has been used to measure the impact of biocontrol in *Asparagus asparagoides*, *Carduus nutans*, *Echium plantagineum*, *Mimosa pigra*, *Onopordum illyricum*, *O. acanthium* and *Sida acuta* (Briese, 2000a). The simple measures of damage alone may not be sufficient to indicate the success of an agent (Farrell & Lonsdale, 1997). The bud-feeding weevil *Trichapion lativentre* reduced seed production in the weed *Sesbania punicea* by 98%, but failed to cause a corresponding decline in the density of mature plants, because the seed loss only removed plants that would have died from competition anyway (Hoffmann & Moran, 1991). This method, though often used to evaluate the impact at the individual plant level, can be used to monitor population changes of the weed if permanent sites are established and monitored over time. However, in weeds where the abundance of biocontrol agents is dependent on plant vigour this method may not be suitable. In *P. hysterophorous*, level of damage by the stem-galling moth *E. strenuana* is dependent on plant size, as a result less vigorous plants escape from gall damage (Dhileepan & McFadyen, 2001). It would be difficult to relate damage levels to plant performance for agents that do not produce obviously visible symptoms, and those feeding in the root zone with inter-plant movement behaviour. In *P. hysterophorus*, damage symptoms of *L. setosipennis* larvae, that bore through the stem as well as feed externally on the root, are difficult to detect. As a result, destructive sampling of plants at the end of a field cage trial revealed no relationship between the number of *L. setosipennis* larval feeding sites and plant vigour and flower production. A sequential destructive sampling is more suitable to measure damage levels of root feeding insects in the field. The main disadvantage of correlating damage levels with plant performance is that the correlations may be due to other unrelated reasons. While relating damage levels with plant performance, we are not manipulating damage levels of randomly selected plants or sites that are otherwise considered equal. In other words, reasons for differences in plant performance are predicted on the basis of damage levels, but not proven. Experimental manipulation of independent variables is required to show that the damage is causing the effect. This method when combined with biocontrol agent and weed population monitoring programs over several seasons at one or more sites would provide an estimate of cause and effect of biocontrol agents (Swirepik & Smyth, these proceedings). This method of evaluation is also less intensive and more suitable for long-term evaluation in perennial and tree weeds where biocontrol exclusion is difficult.

Biocontrol exclusion

Detailed experimental biocontrol exclusion is the preferred method to evaluate the impact of biocontrol agents. The advantage of this method is that it allows rigorous statistical analysis and provides more reliable information than other methods (Farrell & Lonsdale, 1997). However, this method is more costly and time consuming than other methods. Selective sampling of sites with comparable ecological conditions in the presence or absence of biocontrol agents within a region is acceptable at the spatial scale, but may not suitable for long-term evaluation. In parthenium, the impact of defoliation by *Z. bicolorata* can be evaluated by selective sampling of sites with and without defoliation within a property. However, this method has limitations for long-term evaluation, as sites with severe defoliation in one year may not have any defoliation the following year and *vice versa*. To quantify the impact of biocontrol more realistically, excluding the biocontrol agents physically by using exclusion cages or by pesticides, is desirable. Such experimental manipulation removes spatial variation in soil factors, climate, rainfall, grazing pressure, etc.

Biocontrol exclusion using pesticides

This is the most efficient method of evaluation for terrestrial weeds and best suited to small-scale experiments. The advantage of this method is that both treatment and control plots can be at the same site thereby eliminating the spatial variation. This method also provides information on weed density and seed bank if there had been no biocontrol agents. However, this method is labour intensive and expensive, and may not be suitable in certain situations due to pesticide residue problems. This method relies on the periodic application of pesticides, and prolonged wet seasons could increase the need for more frequent pesticide applications, especially for excluding rust fungi using non-systemic fungicides. Hence, this method may not be suitable for areas that cannot be accessed during prolonged wet and flood conditions. Biocontrol exclusion using pesticides has been successfully used to evaluate the effectiveness of biocontrol in *Sida acuta* (Lonsdale *et al.*, 1995), *Mimosa pigra* (Lonsdale & Farrell, 1998) *P. hysterophorus* (Dhileepan, 2001), and *Echium plantagineum* (Sheppard *et al*., 2001).

Biocontrol exclusion experiment in *S. acuta*, using insecticide showed biocontrol had a 11-fold reduction in seed output resulting in 34% reduction in plant density in the following year (Lonsdale *et al.*, 1995). In *M. pigra* biocontrol reduced the seed output, but the insecticides used in the exclusion experiments also had a negative effect on seed production, possibly due to disruption in insect pollination (Lonsdale & Farrell, 1998). However, in similar exclusion experiments on *Chrysanthemoides monilifera* the insecticides had no negative effect on seed production (Adair & Holtkamp, 1999). Exclusion experiments using insecticides showed that biocontrol in parthenium resulted in up to 90% reduction in weed density (Dhileepan, 2001), but the effectiveness of biocontrol was dependent on the agents prevalent and seasonal conditions (K. Dhileepan, unpublished data). In *E. plantagineum* biocontrol exclusion experiment using insecticide revealed that the root-crown weevil *Mogulones larvatus* reduced the plant survival by 43%, and the size and seed weight of survivors by 58% and 74%, respectively (Sheppard *et al.*, 2001).

Biocontrol exclusion using field cages

This method is less efficient compared to exclusion using pesticides and is not suitable for evaluating the impact of pathogens like rust fungi. Field cages can also affect plant vigour, influence agent performance, and exclude the impact of natural enemies (parasites and predators) on the biocontrol agents themselves, resulting in unrealistic results. Evaluation of the impact of *E. strenuana* (Dhileepan & McFadyen, 2001) and *Z. bicolorata* (Dhileepan *et al.*, 2000a) on *P. hysterophorus* in field cages produced results different to the results obtained in pesticide exclusion trials in the field. Hence, results from such studies should be used with caution for broader-scale predictions. It is also difficult to maintain cages in the field for long-term evaluation and the experiments are restricted to the spatial scale of the cages.

Australian experience

In Australia over 60 weeds have been targets of biological control (Briese, 2000a). Evaluations involving agent establishment and abundance have been carried out in majority of the biocontrol programs in Australia. But detailed evaluations have been carried out only in a limited number of biocontrol programs. Among the 164 refereed research publications on the biological control of Australian weeds sampled from Current Contents® (1985-2002), Proceedings of the Australian Weed Conference (Vol.8–13) and Proceedings of the International Symposium on Biological control of Weeds (Vol.5-10), less than 12% of the papers included aspects relating to agent prevalence and impact at the individual plant level. Only 4% of the papers sampled evaluated the impact of biocontrol at weed population level. Quantitative data on the impact of biocontrol is available for 23 weeds (38%) at individual plant level and for 12 weeds (20%) at plant population level (Table 1). However, the Information available on the economic benefits of biocontrol is restricted to *P. hysterophorus* at local scale (Adamson & Bray, 1999), and *Xanthium occidentale* (Chippendale, 1995) and *Echium* spp. (Nordblom *et al.*, 2002) at regional scale.

Future prospects

Evaluation should be an integral part of all ongoing and future biocontrol programs. It is advantageous if all biocontrol programs collect pre-release baseline data on the target weed including the seed bank data. In programs where the agents take several years to become abundant, the pre-release data could also be collected during the agent establishment phase. If possible, this should be supplemented with aerial or satellite photographs of the weed infestation. Where possible, evaluation at the local scale should be linked with the community agencies (i.e. Landcare groups) and a long-term funding commitment from government and other funding agencies. Often evaluations are initiated either as soon as the agents are released or immediately after their field establishment. To obtain realistic results, evaluation should be based on the agents that have already attained their full potential in the field (McFadyen, 1998). Local scale evaluation should focus more on "extensive" studies in varying geo-climatic conditions, than on "intensive" studies in a few areas. This would help in extrapolation of evaluation results from the local to regional scale

Table 1. Evaluation of the effectiveness of biocontrol agents at individual plant and plant population levels in Australia.

Weed	**Agent**	**Impact at plant level**	**Impact at plant population level**
Asparagus asparagoides	*Zygina* sp.	Batchelor & Woodburn, 2002	
	Puccinia myrsiphylli	Morin *et al.*, 2002	
Carduus nutans	*Trichosirocalus horridus*	Woodburn, 1997; 2000	
	Rhinocyllus conicus	Woodburn & Cullen, 1996	
	Urophora solstitialis	Woodburn & Cullen, 1996	
Carduus pycnocephalus & *C. tenuiflorus*	*Puccinia cardui-pycnocephali*		Burdon *et al.*, 2000
Chondrilla juncea	*Puccinia chondrillina*	Hanley & Groves, 2002	
Chrysanthemoides monilifera	*Comostolopsis germana*	Holtkamp, 2002	
Cryoptostegia grandiflora	*Maravalia cryptostegiae* & *Euclasta whalleyi*	Vitelli *et al.*, 1998	Vogler & Lindsay, 2002
Echium plantagineum	*Longitarsus echii*	Smyth & Sheppard, 2002	
	Mogulones larvatus	Sheppard *et al.*, 1999	
	Meligethes planiusculus	Swirepik *et al.*, 1996	
Eichhornia crassipes	*Neochetina burchi* & *N. eichhorniae*	Heard & Winterton, 2000	Wright, 1981
Eriocereus martinii			McFadyen & Tomley, 1981; Tomley & McFadyen, 1985
Hypericum androsaemum	*Melampsora hypericorum*	Casanato *et al.*, 1999	
Hypericum perforatum	*Aculus hyperici*	Jupp & Cullen, 1996	Mahr *et al.*, 1999
	Chrysolina quadrigemina		Clark, 1953; Briese, 1997
	Chrysolina hyperici		Clark & Clark, 1952
	Agrilus hyperici	Briese, 1991	
	Aphis chloris	Briese & Jupp, 1995	
Lantana camara	*Ophiomyia lantanae*	Broughton, 1999	
Mimosa invisa	*Heteropsylla spinulosa*	Ablin, 1995	

Table 1. (cont'd) Evaluation of the effectiveness of biocontrol agents at individual plant and plant population levels in Australia.

Weed	Agent	Impact at plant level	Impact at plant population level
Mimosa pigra	*Neurostr ota gunniella*	Paynter & Hennecke, 2001	Lonsdale & Farrell, 1998; Wilson & Flanagan, 1991
	Phloeospora mimosae-pigrae	Paynter & Hennecke, 2001	
Onopordum spp.	*Larinus latus*	Pettit & Briese, 2000; Briese, 2000b	Swirepik & Smith, 2002
Parkinsonia aculeata	*Penthobruchus germaini*	Lockett *et al*., 1999; Lukitsch & Wilson, 1999	
Parthenium hysterophorus	*Epiblema strenuana*	Navie *et al.* 1998; Dhileepan & McFadyen 2001	Dhileepan, 2001
	Zygogramma bicolorata	Dhileepan *et al*., 2000a	Dhileepan *et al*., 200b; Dhileepan, 2001
	Listronotus setosipennis	Dhileepan 2003	
	Conotrachelus albocinereus	David, 1998	
Pistia stratiotes	*Neohydronomus affinis*		Harley *et al*., 1984
Prosopis spp.	*Algarobius bottimeri* & *A. prosopis*	Donnelly, 2002	
Rubus spp.	*Phrgamidium violaceum*	Mahr & Bruzzese, 1998	
Salvinia molesta	*Cryptobagous salviniae*		Room *et al*., 1981
Senecio jacobaea	*Cochytis atricapitana*	McLaren *et al*., 2000	
	Longitarsus flavicornus		Ireson *et al*., 1991
Sida acuta	*Calligrapha pantherina*	Lonsdale *et al*., 1995	Lonsdale *et al.* 1995; Wilson & Lonsdale, 1995

Suggested protocols

The following generic protocols are suggested for evaluating the effectiveness of biocontrol at local scale:

Aquatic weeds

- Pre and post-release sequential photographs of the weed infestation at yearly intervals. To enable quantification of impact, the photographs should be standardised and calibrated by field measurements. Abundance and damage levels of agents recorded annually at a regional scale with assistance from Landcare and community groups.
- Extrapolate changes in weed infestation levels with biocontrol agent abundance and damage levels.

Terrestrial weeds

- Quantitative pre-release data on the target weed population dynamics (including the seed bank, if relevant).
- Pre and post-release sequential photographs at yearly intervals.
- Score/index the agent abundance annually at a regional scale with assistance from property owners and community groups.
- Monitor the target weed population (seed bank, if relevant) and other vegetation once in 3-5 years
- Relate biocontrol agent damage levels to target weed and other vegetation changes.

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References

Ablin, M.P. (1995). Growth and reproduction of the weed *Mimosa invisa*, in northeast Queensland after introduction of the biocontrol agent *Heteropsylla spinulosa*. Research degree of Master of Science in Tropical Ecology, James Cook University, Townsville, Queensland. pp. 115.

Adair, R.J. & Holtkamp, R.H. (1999). Development of a pesticide exclusion technique for assessing the impact of biological control agents for *Chrysanthemoides monilifera. Biocontrol Science & Technology* **9**, 383-390.

Adamson, D. & Bray, S. (1999). The economic benefit from investing in insect biological control of parthenium weed (*Parthenium hysterophorus*). Natural & Rural System Management, The University of Queensland, Brisbane. pp. 44.

Auld, B.A. (2000). Success in biological control of aquatic weeds by pathogens, including bioherbicides. *Biological control: measures of success* (eds. G. Gurr & S. Wratton), pp. 323-340. Kluwer Academic publishers, The Netherlands.

Batchelor, K.L. & Woodburn, T.L. (2002). Population development and impact of the bridal creeper leafhopper Zygina sp. In Western Australia. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 381-384. Plant Protection Society of Western Australia.

Briese, D.T. (1991). Current status of *Agrilus hyperici* (Coleoptera: Buprestidae) released in Australia in 1940 for the biological control of St John's wort: Lessons for insect introductions. *Biocontrol Science & Technology* **1**, 207-215.

Briese, D.T. (1997). Biological control of St John’s wort in Australia: Past, present and future. *Plant Protection Quarterly* **12**, 73-80.

Briese, D.T. (2000a). Classical biological control: *Australian weed management systems* (ed. B. M. Sindel), pp. 161-192. R.G & F.J. Richardson publishers, Meredith, Victoria 3333, Australia.

Briese, D.T. (2000b). Impact of the *Onopordum capitulum* weevil *Larinus latus* on seed production by its host plant. *Journal of Applied Ecology* **37**, 238-246.

Briese, D.T. & Jupp, P.W. (1995). Establishment and spread of *Aphis chloris* Koch (Hemiptera: Aphididae), introduced into Australia for the biological control of St John's wort. *Biocontrol Science & Technology* **5**, 271-285.

Broughton, S. (1999). Impact of seed-fly *Ophiomyia lantanae* (Froggatt) Diptera: Agromyzidae), on the viability of lantana fruit in south-east Queensland, Australia. *Biological Control* **15**, 168-172.

Burdon, J.J., Thrall, P.H., Groves, R.H. & Chaboudez, P. (2000). Biological control of *Carduus pycnocephalus* and *C. tenuiflorus* using the rust fungus *Puccinia cardui-pycnocephali. Plant Protection Quarterly* **15**, 14-17.

Casanato, S.G., Lawrie, A.C. & McLaren, D.A. (1999). Biological control of *Hypericum androsaemum* with *Melampsora hypericorum*. *Proceedings of the 12th Australian Weeds Conference*, (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp 229-234. Tasmanian Weed Society, Hobart, Tasmania

Chippendale, J.F. (1995). The biological control of Noogoora bur (*Xanthium occidentale*) in Queensland: An economic perspective. *Proceedings of the VIII International Symposium on Biological Control of Weeds* (eds. E.S. Delfosse & R.R. Scott), pp. 185-192. Lincoln University, Canterbury, New Zealand.

Clark, L.R. (1953). The ecology of *Chrysomela gemellata* Rossi and *C. hyperici* Forst., and their effect on St John's wort in the Bright District, Victoria. *Australian Journal of Zoology* **1**, 1-69.

Clark, L.R., & Clark, N. (1952). A study of the effect of *Chrysomela hyperici* Forst. on St John's wort in the Mannus Valley, N.S.W. *Australian Journal of Agricultural Research* **3**, 29-59.

David, J.M. (1998). Efficacy of the stem galling weevil *Conotracheleus albocinereus* as a biological control agent for parthenium weed (*Parthenium hysterophorus L.*). Report of the Department of Natural Resources, Alan Fletcher Research Station, Queensland, Brisbane, Australia. pp. 27.

Dhileepan, K. (2001). Effectiveness of introduced biocontrol insects on the weed *Parthenium hysterophorus* (Asteraceae) in Australia. *Bulletin of Entomological Research* **91**, 167-176.

Dhileepan, K. (2003). Current status of the stem-boring weevil *Listronotus setosipennis* (Coleoptera: Curculionidae) introduced against the weed *Parthenium hysterophorus* (Asteraceae) in Australia. *Biocontrol Science and Technology* **13**, 3-12.

Dhileepan, K. & McFadyen, R.E. (2001). Effects of gall damage by the introduced biocontrol agent *Epiblema strenuana* (Lepidoptera: Tortricidae) on the weed *Parthenium hysterophorus* (Asteraceae). *Journal of Applied Entomology* **125**, 1-8.

Dhileepan, K., Setter, S. & McFadyen, R.E. (2000a). Response of the weed *Parthenium hysterophorus* (Asteraceae) to defoliation by the introduced biocontrol agent *Zygogramma bicolorata* (Coleoptera: Chrysomelidae). *Biological Control* **19**, 9-16.

Dhileepan, K., Setter, S. & McFadyen, R.E. (2000b). Impact of defoliation by the introduced biocontrol agent *Zygogramma bicolorata* (Coleoptera: Chrysomelidae) on parthenium weed in Australia. *Biocontrol* **45**, 501-512.

Donnelly, G. (2002). Two seed-feeding beetles released in Queensland and Western Australia for the biological control of mesquite. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 404. Plant Protection Society of Western Australia.

Farrell, G. & Lonsdale, M. (1997). Measuring the impact of biological control agents on weeds. *Biological control of weeds: theory and practical applications* (eds. M. Julien & G. White), pp. 105-118. Australian Centre for International Agricultural Research, Canberra, Australia.

Forno, I.W. & Julien, M.H. (2000). Success in biological control of aquatic weeds by arthropods. *Biological control: measures of success* (eds. G. Gurr & S. Wratton), pp. 159-187. Kluwer Academic publishers, The Netherlands.

Hanley, M.E. & Groves, R.H. (2002). Effect of the rust fungus *Puccinia chondrillina* TU 788 on plant size and plant size variability in *Chondrilla juncea. Weed Research* **42**, 370-376.

Harley, K.L.S., Forno, I.W., Kassulke, R.C. & Sands, D.P.A. (1984). Successful biological control of water lettuce. *Journal of Aquatic Plant Management* **22**, 101-102.

Heard, T.A. & Winterton, S.L. (2000). Interactions between nutrient status and weevil herbivory in the biological control of water hyacinth. *Journal of Applied Ecology* **37**, 117-127.

Hoffmann, J.H. & Moran V.C. (1991). Biocontrol of a perennial legume, *Sesbania punicea* using a florivorous weevil, *Trichapion lativentre*: weed population dynamics with a scarcity of seeds. *Oecologia* **88**, 574-576.

Hoffmann, J.H. & Moran V.C. (1998). The population dynamics of an introduced tree *Sesbania punicea*, in South Africa in response to long-term damage caused by different combinations of three species of biological control agents. *Oecologia* **114**, 343-348.

Holtkamp, R.H. (2002). Impact of bitou tip moth, *Comostolopsis germana*, on bitou bush in New South Wales. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 405-406. Plant Protection Society of Western Australia.

Ireson, J.E., Friend, D.A., Holloway R.J. & Paterson, S.C. (1991). Biology of *Longitarsus flavicornis* (Stephens) (Coleoptera: Chrysomelidae) and its effectiveness in controlling ragwort (*Scenecio jacobaea L.*) in Tasmania. *Journal of the Australian Entomological Society* **30**, 129-141.

Jupp, P.W. & Cullen, J.M. (1996). Expected and observed effects of the mite *Aculus hperici* on St John's wort, *Hypericum perforatum*, In Australia. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds. V.C. Moran and J.H. Hoffmann), pp. 365-370. The University of Cape Town, South Africa.

Lockett, C., Gray, E. & Donnelly, G. (1999). The prevalence of seed damage by the introduced bruchid, *Penthobruchus germaini* (Coleoptera: Bruchidae), a biological control for Parkinsonia (*Parkinsonia aculeate*) in far north and central Queensland. *Proceeding of the 12th Australian Weeds Conference* (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp. 431-435. Tasmanian Weed Society, Hobart, Tasmania.

Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995). Biological control of a tropical weed: a population model and experiment for Sida acuta. *Journal of Applied Ecology* **32**, 391-399.

Lonsdale, W.M. & Farrell, G. (1998). Testing the effects on *Mimosa pigra* of a biological control agent *Neurostrota gunniella* (Lepidoptera: Gracillaridae), plant competition and fungi under field conditions. *Biocontrol Science & Technology* **8**, 485-500.

Lukitsch, B. & Wilson, A. (1999). Distribution and impact of the mature seed feeding bruchid *Penthobruchus germaini* on *Parkinsonia aculeate* in northern Australia. *Proceeding of the 12th Australian Weeds Conference* (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp. 436-440. Tasmanian Weed Society, Hobart, Tasmania.

Mahr F. & Bruzzese, E. (1998). The effect of *Phragmidium violaceum* (Schultz) Winter Uredinales on *Rubus fruticosus* L. Agg. In south-eastern Victoria. *Plant Protection Quarterly* **13**, 182-185.

Mahr F.A., Mayo, G., Ainsworth, N. & Jupp, P. (1999). Monitoring the impact of the biological control agent *Aculus hyperici* on *Hypericum perforatum* across south eastern Australia. *Proceeding of the 12th Australian Weeds Conference* (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp. 335-338. Tasmanian Weed Society, Hobart, Tasmania.

McClay, A.S. (1995). Beyond "Before-and-after": Experimental design and evaluation in classical weed biological control. *Proceedings of the VIII International Symposium on Biological Control of Weeds* (eds. E.S. Delfosse & R.R. Scott), pp. 213-219. Lincoln University, Canterbury, New Zealand.

McEvoy, P., Cox, C. & Coombs, E. (1991) Successful biological control of ragwort, *Senecio jacobae* by introduced insects in Oregon. *Ecological Applications* **1**, 430-442.

McFadyen, R.E.C. (1998). Biological control of weeds. *Annual Review of Entomology* **43**, 369-393.

McFadyen, R.E.C. (2000). Successes in biological control of weeds. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 3-14. Montana State University, Bozeman, USA.

McFadyen, R.E. & Tomley, A.J. (1981). Biological control of Harrisia cactus, *Eriocereus martini*, in Queensland by the mealybug, *Hypogeococcus festerianus. Proceedings of the V International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 589-594. CSIRO, Australia.

McLaren, D.A, Ireson, J.E. & Kwong, R.M. (2000). Biological control of Ragwort (*Senecio jacobaea L.*) in Australia. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 67-79. Montana State University, Bozeman, USA.

Morin, L., Willis, A.J., Armstrong, J. & Kriticos, D. (2002). Spread, epidemic development and impact of the bridal creeper rust in Australia: summary of results. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 385-388. Plant Protection Society of Western Australia.

Navie, S.C., Priest, T.E., McFadyen, R.E. & Adkins, S.W. (1998). Efficacy of the stem-galling moth *Epiblema strenuana* Walk. (Lepidoptera: Totricidae) as a biological control agent for the ragweed Parthenium (*Parthenium hysterophorus L.*). *Biological Control* **13**, 1-8.

Nordblom, T.L., Smyth, M.J., Swirepik, A., Sheppard, A.W. & Briese, D.T. (2002). Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agricultural Economics* **27**, 403-424.

Paynter, Q. & Hennecke, B. (2001). Competition between two biological control agents, *Neurostrota gunniella* and *Phloeospora mimosae-pigrae,* and their impact on the invasive tropical shrub *Mimosa pigra.. Biocontrol Science & Technology* **11**, 575-582.

Pettit, W. & Briese, D.T. (2000). The demographic performance of the capitulum weevil, *Larinus latus*, on Onopordum thistles in its native and introduced ranges. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp 739-745. Montana State University, Bozeman, USA.

Reznik, S.Y. (2000). What we learned from the failure of the ragweed leaf beetle in Russia. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 195-196. Montana State University, Bozeman, USA.

Room, P.M., Harley, K.L.S., Forno, I.W. & Sands, D.P.A. (1981). Successful biological control of the floating weed salvinia. *Nature* **394**, 78-80.

Sheppard, A.W., Smyth, M. & Swirepik, A. (2001). The impact of *Mogulones larvatus* and pasture competition on *Echium plantagineum. Journal of Applied Ecology* **38**, 291-300.

Sheppard, A.W., Smyth, M.J. & Swirepik, A. (1999). Impact of root-crown weevil (*Mogulones larvatus*) and other biocontrol agents on Paterson's curse in Australia: An update. Proceeding of the 12th Australian Weeds Conference (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp. 343-346. Tasmanian Weed Society, Hobart, Tasmania.

Smyth, M. & Sheppard, A. (2002). *Longitarsus echii* and its impact on *Echium plantagineum* (Paterson's curse): the insect for the Mediterranean rainfall range of the weed?. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 422-425. Plant Protection Society of Western Australia.

Swirepik, A.E., Sheppard, A.W. & Smyth, M.J. (1996). *Meligethes planiusculus* (Heer) (Nitidulidae) an inflorescence-feeding beetle, with good potential as a biocontrol agent for *Echium plantagineum. Proceedings 11th Australian Weeds Conference*, (ed. R.C.H. Shepherd), pp. 294-297.

Swirepik, A. & Smyth, M. (2002). Biological control of broad-leafed pasture weeds (Paterson's curse, *Onopordum* and nodding thistles): what have we achieved and where to from here? *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 373-376. Plant Protection Society of Western Australia.

Syrett, P., Briese, D.T. & Hoffmann, J.H. (2000). Success in biological control of terrestrial weeds by arthropods. *Biological control: measures of success* (eds. G. Gurr & S. Wratton), pp. 189-230. Kluwer Academic publishers, The Netherlands.

Tomley, A.J. & McFadyen, R.E. (1985). Biological control of Harrisia cactus, *Eriocereus martini*, in central Queensland by the mealybug, *Hypogeococcus festerianus*, nine years after release. *Proceedings of the VI International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 843-847. Agriculture Canada, Vancouver, Canada.

Vitelli, M., Tomley, A., Lindsay, A., Lowe, R., Lockett, C., Gray, E., Setter, C., Madigan., Williamson, K. & Mayer, B. (1998). Rubber vine bioevaluation – insect and rust population dynamics. 1997-98 Technical highlights. Pest management research, Department of Natural Resources, Queensland. pp. 30-32.

Vogler, W. & Lindsay, A. (2002). The impact of the rust fungus *Maravalia cryptostegiae* on three rubber vine (*Cryptostegia grandiflora*) populations in tropical Queensland. *Proceeding of the 13th Australian Weeds Conference* (eds. H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 180-182. Plant Protection Society of Western Australia.

Wilson, C.G. & Flanagan, G.J. (1991). Establishment of *Acanthosceilides quadridentatus* (Schaeffer) and *A. puniceus* Johnson (Coleoptera: Bruchidae) on *Mimosa pigra* in northern Australia. *Journal of the Australian Entomological Society* **30**: 279-280.

Wilson, C.G. & Lonsdale, W.M. (1995). Biological control of *Sida acuta* in Australia's Northern Territory. *Proceedings of the VIII International Symposium on Biological Control of Weeds* (eds. E.S. Delfosse & R.R. Scott), pp. 451. Lincoln University, Canterbury, New Zealand.

Woodburn, T.L. (2000). Effectiveness of *Trichosirocalus horridus* against *Carduus nutans* in Australia. *Proceedings of the X International Symposium on Biological Control of Weeds* (ed. N.R. Spencer), pp. 780. Montana State University, Bozeman, USA.

Woodburn, T.L. (1997). Establishment in Australia of *Trichosirocalus horridus* a biological control agent for *Carduus nutans*, and preliminary assessment of its impact on plant growth and reproductive potential. *Biocontrol Science & Technology* **7**, 645-656.

Woodburn, T.L. & Cullen, J.M. (1996). Impact of *Rhinocyllus conicus* and *Urophora solstitialis* on seed-set in *Carduus nutans* in Australia. In Compositae: Biology and Utilization. *Proceedings of the International Compositae Conference* (eds. P.D.S. Caligari & D.J.N. Hind), Vol. 2, pp 307-319. The Royal Botanic Gardens, Kew, UK.

Wright, A.D. (1981). Biological control of water hyacinth in Australia. *Proceedings of the V International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse), pp. 529-535. CSIRO, Australia.

Evaluating biological control at the regional scale

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Summary

Weeds that become targets for biocontrol projects often have a wide invaded distribution. The scale of the distribution offers a challenge to researchers for monitoring the outcomes of the project. A three-tiered structure for evaluation is described (using the *Echium plantagineum* project as a model), where Tier one provides robust relationships on plant and agent performance, Tier two provides key performance data derived from the relationships gathered in Tier one and allows for predictions on impact to be made, and Tier three provides easily collected data on agent establishment and dispersal. Tier one evaluation is the responsibility of the primary research group and is usually carried out at a limited number of sites. Tier two monitoring is carried out on a regional scale where sites are selected to represent the performance of agents in a particular climatic zone (or otherwise functionally discreet area); this work will usually involve officers from other collaborating organisations (such as state agricultural departments). The monitoring of establishment and dispersal, i.e. Tier three, should be carried out at all release sites, and usually involves input from the primary researchers, state departments, local government and community stakeholders. The information gathered at all levels should be captured centrally by the primary research group. This information will provide decision support for ongoing release programs (i.e. targeting an agent to suitable climatic regions and land management types), which will in turn maximise impact and provide an estimate of this impact over the entire distribution of the weed.

Key words: Biocontrol of weeds, impact evaluation, regional scale, three-tiered structure

Introduction

In the past, evaluation of weed biocontrol outcomes have been scant due to the perception that such activities are an expensive luxury, especially in the light of classic Australian successes such as *Opuntia*, *Chondrilla* and *Salvinia*. Unfortunately, this has led to a poor understanding of why projects succeed, fail or achieve intermediate results. Such information would not only provide better justification for biocontrol funding, but would also inform the agent selection process for subsequent projects and provide gateways to integrating biocontrol with other management practices.

If the discipline of weed biocontrol is to prosper into the future, then researchers need to build evaluation into the cost of a project from its inception. For this to be palatable to funding bodies in an era of financial probity, evaluation needs to be clearly defined, appropriately targeted and provide data that cover agent establishment, spread and impact. Often the scale of a weed's distribution is too large for the collection of these data solely by the principal research group to be practical (e.g. *Echium plantagineum* (L.), *Asparagus asparagoides*, (L). Willd). In such instances collaboration is essential and identifies a perfect role for coordinating agencies such as the Cooperative Research Centre for Australian Weed Management (CRC).

In 1996 the CRC conducted a workshop (in Yanco NSW) with the aim of developing a structure for the collaborative evaluation on biocontrol. A key outcome of the workshop was the need for a hierarchical structure to allow collaborators to collect data commensurate with their skill and level of commitment to the project. The data then must fit together to provide the overall picture. To this end we describe a three-tiered structure that implements the outcomes from the Yanco workshop, where Tier one provides the most detailed information that defines agent impact, Tier two measures both agent and target population dynamics and Tier three measures establishment and spread.

Tier one evaluation

Tier one data are the responsibility of the primary research group involved in the project. The key outcome of Tier one is to provide robust measures of the impact of each agent on the target species. To achieve this it is often necessary to identify and quantify key transition-stage relationships for the target (Woodburn and Cullen, 1993; Sheppard *et al.*, 1994; Woodburn and Cullen, 1996; Smyth *et al.*, 1997; Briese, 2000; Sheppard *et al*,. 2001; Briese *et al.*, 2002). For example, in the case of the annual broad-leafed pasture weed, *Echium plantagineum*, a suite of four agents have been selected for continued redistribution. Three of the agents

(*Mogulones larvatus* Schultze (Coleoptera: Curculionidae), *M. geographicus* Goeze (Coleoptera: Curculionidae) *and Longitarsus echii* Koch (Coleoptera: Chrysomelidae) attack the crown and root zone of the plant during the growing season influencing plant size and therefore seed production. The fourth agent, the pollen beetle, *Meligethes planiusculus* Heer (Coleoptera: Nitidulidae), attacks the flowering cyme and has a direct effect on seed production.

Collecting seed production data for *E. plantagineum* is time consuming and labour intensive, so to streamline data collection several key relationships have been developed as a part of Tier one evaluation. The first is the relationship between the numbers of seed produced per plant per unit of flowering cyme length (mm) (Figure 1). Data collection involved counting individual seeds produced in each calyx along the length of a sub sample of flowering cymes per plant, at multiple sites over multiple years. Seed production is also sequential as the cyme elongates throughout the flowering season which requires sampling on a fortnightly basis throughout the season so that no seed are missed (Smyth *et al.*, 1997).

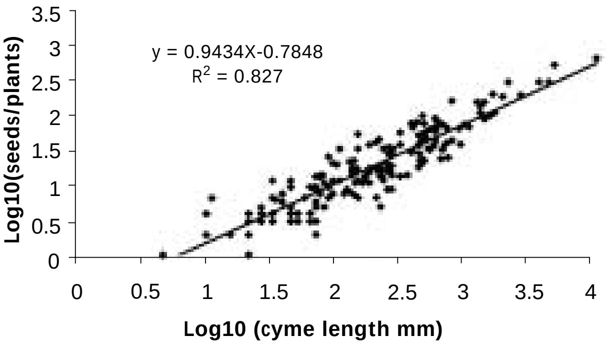

Figure 1. The relationship between *E. plantagineum* flowering cyme length and seed per plant (log scale). Data collected from sites at Jugiong and Tarcutta, NSW 1992-1994.

Another relationship was based on the number of seed produced per plant per unit of taproot size, measured as taproot diameter just below the crown (Figure 2). Data collection for this relationship initially involved counting all seeds on a sub sample of cymes to add additional validation to the seed per cyme relationship. Once the first year's analysis was complete a decision was taken to only measure cyme length in subsequent samples and rely on the seed per cyme length relationship to estimate seed production. Plant weights were also sampled and there is a relationship here between plant weight and taproot diameter as described by the equation below:

Log_{10} (shoot wt) = 1.643 x Log_{10} (taproot Ø) - 1.0177

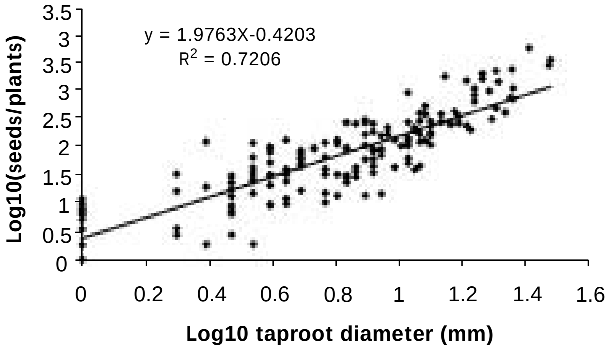

Figure 2. The relationship between the tap toot diameter of *E. plantagineum* and seed produced per plant. Data collected at 5 sites in NSW, 1992-94.

The data presented provide clear examples of quantifying key plant parameters so that simple plant measures may be used to accurately estimate vegetative or reproductive output.

Mogulones larvatus At the same time as the plant relationships were being quantified, research was also being carried out to measure the effects of the crown weevil, *M. larvatus,* on *E. plantagineum* size and seed production. This work was initially carried out as a manipulative "garden" experiment and was conducted over two years. The experiment involved comparing seed production of attacked and unattacked plants (a chemical exclusion was used) in the presence or absence of pasture competition (Sheppard *et al.* 2001), (Figure 3).

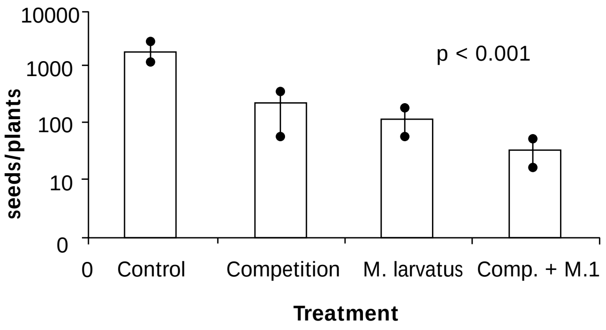

Figure 3. Impact of *M. larvatus* and plant competition on *E. plantagineum* seed production

The benefits of conducting a garden experiment are not just restricted to their predictive value for likely agent impact. Controlled impact experiments allow conformation of plant relationships described above under an increasing level of agent attack. In the case of *M. larvatus* on *E. plantagineum* its impact is to reduce plant size and subsequent seeding without changing the plant relationships. Controlling for agent dependent effects on plant parameter relationships is vital if these are to be used sensibly in predicting agent impact.

The final stage in Tier one evaluation is to draw the link between agent number per unit of host plant and any reduction in plant size, seeding and mortality. Robust relationships here allow simplified sampling of agent impact on its host across the distribution of the weed. In the example of *M. larvatus* on *E. plantagineum*, quantifying the percentage of plants attacked in a population provides a reasonable predictor of plant mortality (Figure 4).

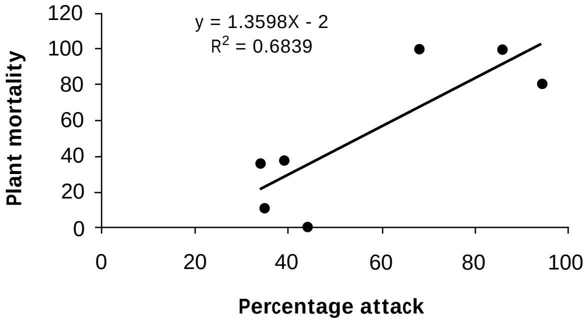

Figure 4. Attack rate of *M. larvatus* on *E. plantagineum* in winter and subsequent plant mortality.

Quantifying larval number and plant size greatly improves the accuracy of predicting agent impact (Figure 5). When these additional parameters (larval load and plant size) are measured for field populations, the confidence in predicting plant mortality (or whatever parameter you wish to measure) is significantly improved (Figure 6). This extra detail will also be necessary for agents that have less impact on their host than *M. larvatus*, i.e. those that do not have the ability to cause plant mortality, but simply limit plant size and subsequent reproductive output. It is worth noting that the estimates of these relationships are not static; as additional data are collected between years and sites, the estimates are continually improved.

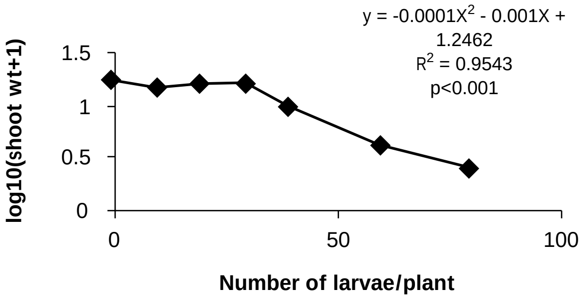

Figure 5. Relationship between the number of *M. larvatus* larvae and the reduction in *E. plantagineum* size.

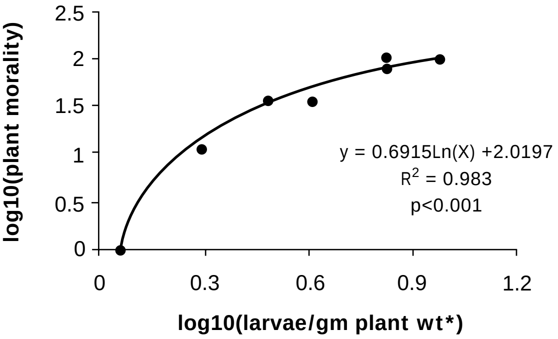

Figure 6. The relationship between *M. larvatus* larvae number and *E. plantagineum* size and subsequent plant mortality.
*Plant wt predicted from taproot regression

Mogulones geographicus The root weevil *M. geographicus* is an example of an agent whose damage rarely causes plant mortality. Instead, larval damage is more subtle and largely occurs under ground on the taproot, causing a reduction in plant size and reproductive output. The relationship in Figure 7 will allow the prediction of *M. geographicus* impact.

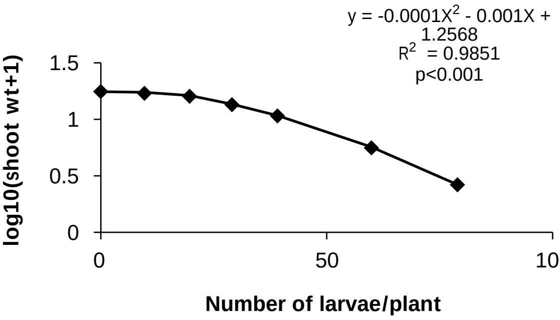

Figure 7. The relationship between *M. geographicus* larval number and the reduction in *E. plantagineum* size.

Longitarsus echii *L. echii* is another root feeding agent whose impact in a controlled field experiment has been studied. Like *M. larvatus*, its impact is to reduce plant size. It does not change the allocation to vegetative and reproductive plant structures (Smyth & Sheppard, 2002). Quantifying the relationship between the number of *L. echii* larvae and plant size is about to commence in the laboratory and at field sites where larval load is high.

Meligethes planiusculus Tier one evaluation for this species has not yet commenced as it is the least well established agent in the suite and is having only minor local impact on *E. plantagineum*. Tier one evaluation will revolve heavily around the relationship described in Figure 1, i.e. changes to the seed/cyme length (or seed per calyx) relationship that will describe its impact. In this instance, the relationship between seed/cyme length will be vital for the quantification of impact, as both adults and larvae of *M. planiusculus* affect seed production. This will make any attempt to quantify impact by exclusion through either chemical or physical means virtually impossible. If a chemical exclusion is attempted the chemical will only exclude larval feeding damage, while using a cage or similar to exclude *M. planiusculus* adults will effect pollination (Swirepik *et al.*, 1996).

Tier two monitoring

The monitoring of agent performance in Tier two draws directly on the relationships developed in Tier one. The advantage here is the ease with which sites can be monitored using simple one off measures. In the case of *M. larvatus*, recording the weed density and the rate of attack in late winter predicts weed mortality successfully. For other insect species, this simple relationship may not be enough to predict impact on a weed. The additional effort of recording plant size and insect number will be a more accurate measure of impact and may be necessary for most insect species (Figures 5-7). The sampling of sites in this way allows data from many sites, across climatic and land management practices to be monitored relatively quickly and accurately, through engaging officers from state agricultural departments to collect these data.

An example of Tier two data is shown in Figure 8 where *M. larvatus* mean population growth is followed through time. When sub samples of this data are analysed, the impact of factors such as grazing management and or climate can be measured. Conversely, it is possible to predict that, at sites where the maximum attack rate was attained in 2000/01, approximately 50% of plants will have been killed by *M. larvatus* before the onset of flowering. These data are also valuable to the redistribution aspect of the project, since they identify rapidly expanding agent populations, which inturn provides the ability to predict when a release site may be ready for collection and redistribution (Swirepik & Smyth, 2002).

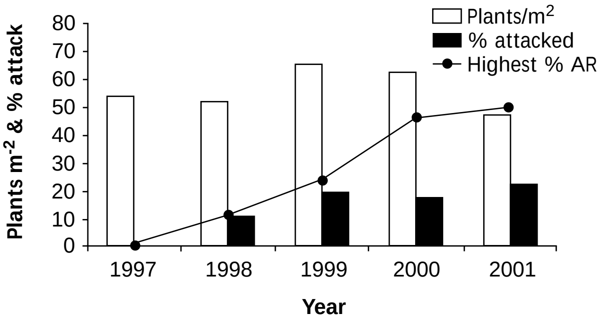

Figure 8. Tier two monitoring for *M. larvatus* and *E. plantagineum* 1997-2001 (40 sites sampled across temperate Australia).

The information gathered through Tier two monitoring on *M. larvatus* has also influenced the design of an integrated weed management experiment which looks at ways to maximise the impact of *M. larvatus* in grazing pasture through providing tactical grazing options (Huwer *et al.*, 2002).

As with *M. larvatus*, the Tier two monitoring for *M. geographicus* and *L. echii* will be closely linked to the relationships developed in Tier one evaluation. Unlike *M. larvatus*, a simple one off measure of attack rate may not be enough to confidently predict a reduction in plant size or survivorship. Sampling may need to include measures of plant size, such as taproot diameter and number of larvae per plant. The additional information gathered should then allow a single sample per site to predict impact on *E. plantagineum*.

The Tier two monitoring for *M. planiusculus* is yet to be finalised but will undoubtedly involve the seed and calyx per cyme length relationships quantified in Tier one (Figure 1). Changes in these reproductive relationships, relative to the number of larvae and adult *M. planiusculus* will form the basis of this monitoring.

Tier three monitoring

Tier three monitoring is in many ways the simplest form of evaluation in a biocontrol project. Its aim is to provide information on the establishment (see Table 1) and spread of agents at all release sites. The essential element in collecting these relatively simple data is to provide all collaborators in the project with the skills needed to recognise the biocontrol agent and the symptoms it causes on the target post release.

Table 1. Establishment rates (%) for *Echium* agents.

Agent	WA	SA	VIC	NSW
M. larvatus	16	26	66	60
M. geographicus	47	33	17	80
L. echii	80	70	60	80
M. planiusculus	18	50	40	29

This technical transfer exercise is in itself a multi- tiered process that begins with CSIRO Entomology officers training state (agriculture departments / Landcare) and local government officers (weeds officers or similar) as well as community collaborators (primarily graziers in this case). State agriculture officers that receive primary training are then formally responsible as a part of the project for the secondary training of all collaborators (professional or community) that they engage in the project. Although not formalised, there is evidence that indicates secondary collaborators such as Landcare coordinators, weeds officers and graziers have taken ownership of the biocontrol agents and provided a tertiary level of training to new collaborators on release and Tier three monitoring techniques.

Once collaborators have observed establishment they are then encouraged to walk in radiating circles around the release and assess the spread of the agent. This information then feeds back into a central data base which is collated at CSIRO Entomology. These data are then used together with Tier two data on population growth to support decisions on the location and total number of releases required to provide maximum coverage of the agents.

A direct outcome of Tier three monitoring is how it influences agent release strategies. For example, based on the regional Tier three monitoring, the project no longer recommends the release of *M. larvatus* in drier/late-break areas infested with *E. plantagineum.* Instead, the release of *M. geographicus* and especially *L. echii* is encouraged in these areas due to their naturally longer aestivation period, which allows them to remain dormant through prolonged autumn drought and has led to higher establishment rates (Table 1).

Tier three monitoring has also demonstrated that the size (number of agents) and timing of a release influenced the chances of establishment. The observations recorded here in Tier three were later confirmed through experimental work in Tier one (unpublished data). The experimental work confirmed positive trends on insect establishment for the size of agent release and the season of release, i.e. the establishment of autumn releases is superior to spring releases.

Regional evaluation

When related back to the three-tiered evaluation structure described above, evaluating biocontrol at the regional scale will be primarily focused on collecting data from Tiers two and three. In the example of *M. larvatus* and *E. plantagineum*, the responsibility for the collection of these data is also broken up on a regional scale, i.e. officers from CSIRO Entomology and the state departments are each responsible for the collection of Tier two data from their state or region. The same officers are also responsible for the collection and / or collation of Tier three data for their state or region, and this exercise (as described above) involves coordinating the activities of local collaborators.

Evaluation outside of the three-tiered structure

The need for evaluation outcomes at the regional level may not always be driven by the primary research group. One such example is currently occurring with *Asparagus asparagoides* (bridal creeper), a declared Weed of National Significance (WONS). WONS status gained *A. asparagoides* a national steering committee and access to National Heritage Trust (NHT) funding. NHT not only provided funding for the redistribution of the biocontrol agents (the leaf hopper, *Zygina sp.*, and the rust, *Puccinia myrsiphylli*) (Woodburn *et al.*, 2002), but also provides funding for on-ground work by community groups. The bridal creeper national steering committee prepared a benchmark monitoring protocol for use by community groups to measure changes in vegetation structure and biocontrol agent population dynamics at control sites (http://www.ento.csiro.au/bridalcreeper/monitoring).

These data will then be collated by a state coordinator for reporting back to Environment Australia, with the primary goal of justifying expenditure and enhancing the prospects of future funding applications.

The weak point in this process is that there is no medium- to long-term funding for the central coordination of data collection, validation and analysis, either through a funded national coordinator or through the primary biocontrol research group (CSIRO Entomology). As a consequence, any data collected is in danger of being archived and forgotten, rather than used to help determine the ultimate outcomes of NHT expenditure. This issue needs to be addressed.

Discussion

Rather than being viewed in isolation, evaluation at the regional scale needs to be seen as an integral part of an overall evaluation program. The three-tiered structure described above provides a functional and dynamic model on which this can be based (Figure 9). The structure in this example has provided many benefits to the *Echium* project, the discipline of biocontrol and also the broader discipline of weed management. In Tier one, we gained a high level of understanding of the key plant performance relationships for *E. plantagineum*, and the impact that the suite of agents has on these relationships. These data have then provided the backbone for Tier two and three monitoring to be carried out in a cost effective manner across temperate Australia through a network of professional and community collaborators.

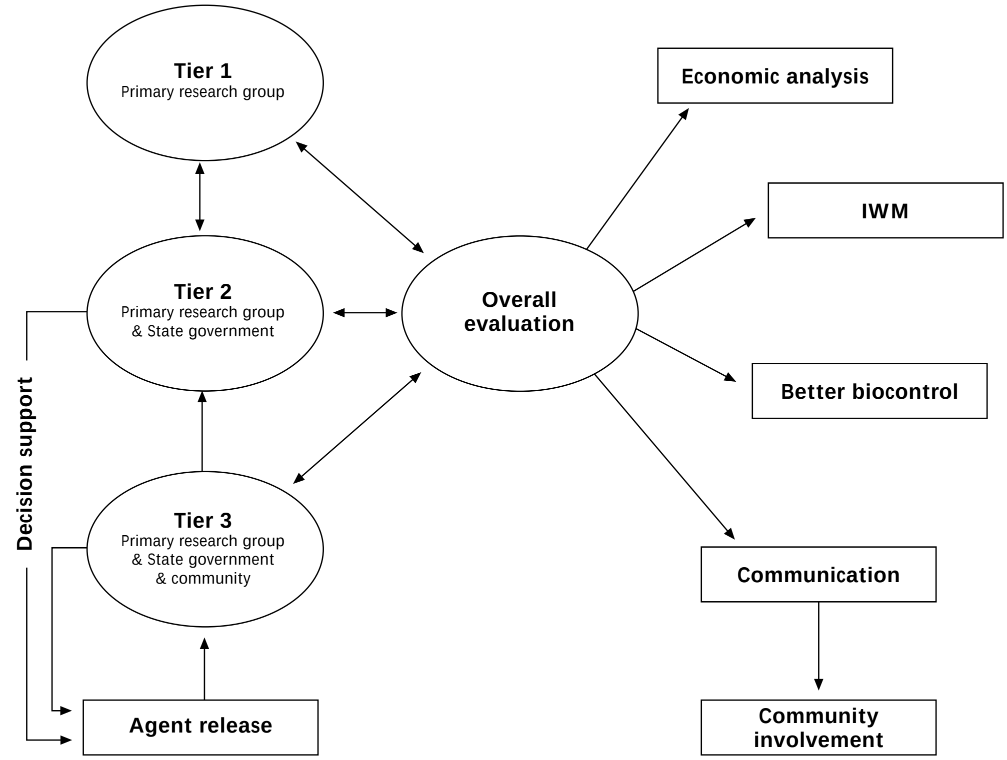

Figure 9. Schematic representation of evaluation process and outcomes.

For *E. plantagineum* the data set has: 1) provided a decision support framework that has facilitated the targeting of agent releases to areas where they are best suited, and informed how to best release those agents, 2) given the ability to predict the time frame over which project outcomes may be realistically expected; 3) played an integral role in the extension of the project to community collaborators; and 4) provided a sound justification of project expenditure to our funding partners that has realised a long-term partnership.

The discipline of biocontrol has benefited from the monitoring program through the insights gained into how a suite of agents impacts on their host and how this will in turn influence field population dynamics. This knowledge will add decision support to agent selection for future projects.

The broader discipline of weed control has gained from the monitoring program through a contribution to the design and implementation of an Integrated Weed Management experiment conducted on three broad leafed pasture weeds *E. plantagineum*, *Onopordum* spp. and *Carduus nutans* over the past four years. In this case, data from the analogous thistle evaluation programs also fed into the experiments. Unfortunately, this leading edge work is coming to an end this September 2002, as it is considered too avante garde by the primary funding corporations and yesterdays news by the new National Cooperative Research Centre structure.

Data from the evaluation project has also been used in an economic analysis. To add biological reality to the analysis, the regional impact of *M. larvatus* from Tier two and spread data from Tier three, were used to estimate economic benefit (Nordblom *et al.*, 2002). The biological reality built into this analysis through the union of agent monitoring and economics separates it from previous more simplistic economic analyses of biological control, where agents were typically given an arbitrary rate of spread and impact. The spatial component of the economic analysis proved valuable, in highlighting the need for investment in additional targeted releases of *M. larvatus* (in areas where release numbers are low and potential benefits are high) to speed up the control of *E. plantagineum*.

All of these benefits have not been derived without some difficulty; the main difficulty is anthropocentric and natural enough in a collaborative project where we have formed complex collaborative links with two levels of government and the community across four states and one territory. Within these jurisdictions, there are collaborators from many different backgrounds and organisational cultures, all of whom require a level of technical understanding about the project commensurate with their level of involvement. At times, the effective delivery of this knowledge has been disproportionately time consuming and frustrating. However, the end result is a functional project worthy of both the long-term past investment, and the medium term investment currently required to complete it.

Acknowledgments

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References

Briese, D.T. (2000) Impact of the *Onopordum* capitulum weevil *Larinus latus* on seed production by its host-plant. *Journal of Applied Ecology* **37**, 1-10.

Briese, D.T., Thomann, T. & Vitou, J. (2002) Impact of the rosette crown weevil *Trichosirocalus briesei* on the growth and reproduction of *Onopordum* thistles. *Journal of Applied Ecology* **39**, 688-698.

Huwer, R.K., Neave, M.J., Dowling, P.M., Lonsdale, W.M., Sheppard, A.W., Briese, D.T. & Michalk, D.L. (2002) Integrated weed management (IWM) in perennial pasture using pasture and grazing management, herbicide strategies and biological control. *Proceedings of the 13th Australian Weeds Conference,* (eds. H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 727-730.

Nordblom, T.L. Smyth, M.J., Swirepik, A.E., Sheppard, A.W. & Briese, D.T. (2002) Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agricultural Economics* **27**, 403-424.

Sheppard A.W, Smyth, M.J. & Swirepik, A.E. (2001) The impact of Mogulones larvatus and pasture competition on *Echium plantagineum. Journal of Applied Ecology* **38**, 291-300

Sheppard A.W., Cullen J.M. & Aeschlimann, J.P., (1994) Predispersal seed predation on *Carduus nutans* (Asteraceae) in southern Europe. *Acta Oecologia* **15**, 529-541.

Smyth, M.J., Sheppard, A.W. & Swirepik, A.E. (1997) The effect of grazing on seed production in *Echium plantagineum. Weed Research*, **37**, 63-70.

Smyth, M.J. & Sheppard, A.W. (2002) *Longitarsus echii* ands it impact of *Echium plantagineum* (Paterson's curse), the insect for the Mediterranean range of the weed. *Proceedings of the 13th Australian Weeds Conference*, (eds. H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 422-425.

Swirepik, A.E. & Smyth, M.J. (2002) Biological control of broad-leafed pasture weeds (Paterson's curse, *Onopordum* and Nodding thistles). What have we achieved and where to from here? *Proceedings of the 13th Australian Weeds Conference*, (eds. H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 373-376.

Swirepik, A.E., Sheppard, A.W. & Smyth, M.J. (1996) *Meligethes planiusculus* (Heer) (Nitidulidae) an inflorescence-feeding beetle, with good potential as a biocontrol agent for *Echium plantagineum. Proceedings 11th Australian Weeds Conference*, (ed. R.C.H. Shepherd), pp. 294-297.

Woodburn, T.L. & Cullen, J.M. (1993) Effectiveness of *Rhinocyllus conicus* a biological control agent for *Carduus nutans*, in Australia. *Proceedings of the 14th Asian – Pacific Weed Conference*, (ed. J.T. Swarbrick), pp. 99-103.

Woodburn, T.L. & Cullen, J.M. (1996) Impact of *Rhinocyllus conicus* and *Urophora solstitialis* on seed set in *Carduus nutans* in Australia, *Compositae: Biology and Utilisation conference. Proceedings of the International Compositae Conference* Vol 2, (eds. P.D.S. Caligari and N.J. Hind), pp. 307-319.

Woodburn, T.L., Morin, L., Batchelor, K., Swirepik, A.E. & Armstrong, J. (2002) Enhancement of biological control of bridal creeper by using community as a resource. *Proceedings of the 13th Australian Weeds Conference*, (eds. H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 701-703.

The roles of ecological models in evaluating weed biological control agents and projects

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Summary

In some limited cases, the results of a classical biological control introduction are spectacular and unambiguous. Indeed, such legendary cases continue to fuel the support for this form of weed control amongst land managers and policy makers in spite of generally uninspiring success rates for introductions, and growing concerns about risks. In most cases, successfully introduced and established biological control agents affect their target weed populations in an unspectacular manner. The use of properly designed experiments to demonstrate the direct effects of biological control agents on plant populations has been forcefully argued, and there are strong advocates for the use of models as an aid to agent selection. The potential roles of ecological models in the evaluation of introduced control agents are less intuitive. They provide a framework with which to design an appropriate set of experiments to gauge impact, and a means of synthesising the results; scaling up the proximal plant-level agent impact measurements into dynamic population-level predictions of weed behaviour. They provide an insight into the various roles and value of the agent as it affects the different aspects of the invasion, colonisation, occupation and reoccupation of sites by weeds. Models can provide an understanding of the mechanisms underlying variation in agent impact in different habitat types. They can also be used to design effective, parsimonious, low-risk integrated weed management systems. Finally, ecological population models can bridge the gap between proximal agent effects and economic analyses.

Key words: biological control, ecological modelling, population dynamics, risk

Introduction

The calls for evaluations of the weed control impacts of both potential and introduced biological control agents have been increasing in frequency and intensity. Such calls appear to have been driven primarily by interrelated concerns regarding accountability (McClay 1995), efficiency (Pantone *et al.*, 1989; McEvoy & Coombs 1999), and risks to ecosystems and non-target organisms associated with the intentional translocation of exotic organisms (Simberloff & Stiling 1996; Louda *et al.*, 1997). To comprehensively address these concerns we therefore need to undertake biological control programs in a manner that demonstrably delivers effective, parsimonious systems that pose minimal or acceptable risk to ecosystem functions and non-target organisms (McEvoy & Coombs, 1999). There are two distinct components to this undertaking: firstly, the development of good biological control systems, and secondly, the demonstration of their desirable features (i.e., negative impacts of agents upon weed abundance). Ecological modelling has much to offer the biological control community in addressing each of these components (Table 1).

Each translocation of an exotic organism carries with it risks of unintended consequences such as damage to non-target organisms or secondary ecological effects that impact upon ecosystem function. Therefore, reducing the number of agents that are imported lowers the risk of unintended consequences. In consideration of the high costs of importing and testing agents, the fewer agents used to achieve successful control of the weed, the greater the efficiency of the project.

There is an on-going debate as to whether a successful weed control project usually follows a *lottery* model, or a *cumulative stress* model. Under the lottery model, one agent is primarily responsible for bringing the target weed under control in a given environment (Myers, 1985; Denoth *et al.*, 2002). The alternative argument is that successful control may be achieved by the combined effects of multiple agents. In both cases, a naive conclusion is that introducing more agents increases the chances of success. In the lottery model the greater the number of agents introduced and established, the greater the chances of finding that one effective agent. In the cumulative effects model, the more agents that are introduced, the more likely it is that the required mix of agents' guilds is represented. This "more is better" imperative is supported by the findings of Denoth *et al.* (2002) that the probability of achieving successful control of weeds was significantly related to the number

Table 1. Applications of models in evaluation of agents for biological control.

Application / Model Type	Pre-importation agent prioritisation	Pre-importation agent prioritisation	Agent redistribution
Climate	Climate-matching? Geographic range of agent and weed Economic value of agent	Geographic range of agent and weed Economic value of agent	Targeted release strategy recognising relative habitat suitability for agent
Population Dynamics			
Analytical	Lifestages worth attacking Scaling-up observations from individual plant to population level and rate of invasion	Retrospective analyses Scaling-up observations from individual plant to population Demonstrating subtle impacts	
Process-based	Advantages of both matrix model and phenological development models with better ability to simulate other management factors	As for transition matrix, but capable of considering multiple sites and can better deal with other management factors	
Transition Matrix	Identifying general principles to aid in agent prioritisation and selection	Explaining reasons behind failures and successes	
Phenological Development	Phenological synchronicity of agent and weed under different climates indicates when control may be exerted in different locations	Understanding agent failure	
Competition Models (inverse linear models)	Relative impact of different agents and other factors (e.g., competition) on weed parameters	Relative impact of different agents and other factors (e.g., competition) on weed parameters Identifying subtle impacts	

of species released, though only 23% of variation was explained by this factor. This imperative is clearly at odds with the risk minimisation imperative, and may also carry with it risks to the biological control project itself in terms of revenge effects e.g., negative interactions between agents, weed replacement, or negative non-target effects (McEvoy & Coombs, 1999).

In order to reconcile the joint imperatives of achieving successful control and coincidently minimising risks and costs, it is necessary to get better at choosing agents for importation. Host-specificity testing procedures have improved in recent times (Withers *et al.*, 2000), providing a better understanding of the likely risks of non-target damage posed by potential control agents. In addition, the social and political value placed upon non-target damage to native plants has increased (Briese, these proceedings). This is likely to result in greater precaution in choosing agents for importation. Unfortunately, these efforts to increase our understanding and management of the potential costs have not been mirrored by efforts to better understand and predict the potential benefits of putative biological control agents (McEvoy & Coombs, 1999). It is only when the likely costs and benefits of an introduction are understood, that a balanced decision can be made as to whether to proceed with an introduction.

Predicting the benefits of introducing an organism as a biological control agent requires well-designed experiments to be undertaken (McClay, 1995) and the development of ecological models (Pantone *et al.* 1989; McEvoy & Coombs, 1999). However, there have been few published examples of this having been done prior to agent introduction for either insect pests (Godfray & Waage, 1991) or weeds (Hoffmann, 1990). In this context, ecological models can be used to predict the potential geographical range of the putative control organism, and the likely population-level impact upon the target weed. At the very least, this approach should allow us to reduce the number of ineffective agents. A population model of the weed can also be used to identify an 'Achilles heel' in the lifecycle of the plant, should it exist, or to explore the options for designing a biological control system with minimal redundancy i.e., containing the minimum number of agents required to achieve successful control (McEvoy & Coombs, 1999).

The need to demonstrate the success of biological control projects is obviously necessary to maintain investor confidence in the ability of the technology to deliver benefits, and the associated financial support for future and on-going projects (Swirepik and Smyth, this proceedings). Few weed biological control projects achieve success with their first or second introduced agent. Maintaining investor confidence in biological control requires compelling contemporary and preferably parochial evidence that success is close at hand.

Understanding the impact of an agent on the target weed population is an important component of a biological control project, which can influence the decision-making process regarding the importation or release of additional agents. Understanding the impact of introduced control agents on weed population dynamics is also a vital component of any process of improving the science of biological control.

Developing effective, efficient, low-risk biological control systems

Prioritising agents

The introduction of all possible control agents is becoming an increasingly untenable strategy due to the risks of non-target and other revenge effects, and the economic reality that all potential agents are unlikely to be able to be imported. Therefore efforts aimed at prioritising agents for processing is clearly warranted. Current protocols for evaluating and prioritising potential biological control agents (Harris, 1973; Goeden, 1983; Wapshere, 1985; Crawley, 1986; Crawley, 1989) are clearly inadequate. They focus attention on attributes of the agent, ignoring attributes of the ecology of the target weed and they provide conflicting advice (Blossey, 1995).

Whilst weed population dynamics models can't account for all the factors affecting agent establishment and efficacy in a new environment, they can aid in understanding some of the attributes of a successful agent in terms of its impacts upon different lifestages of the plant (McEvoy & Coombs, 1999; Kriticos *et al.*, 1999).

Not all lifestages in a plant lifecycle are equally important in maintaining or expanding its presence in a community or its ability to invade new territory. Elasticity analyses of population dynamics models can reveal which lifestage transitions are the most important in maintaining a weed population under various circumstances. Successfully introduced agents that attack sensitive lifestages are likely to be able to exert more control on the weed population than those that affect stage transitions that are relatively insensitive or robust. At worst, this approach would be able to identify agents that were highly unlikely to exert satisfactory control upon a target weed. At best, it would identify agents or guilds that would likely exert sufficient control on the plant if they become established and prevalent in reasonable numbers; identifying those species most worthy of processing for import and further testing.

In any assessment of potential or real agent impact, it is crucial to carefully define what attributes of the plant population make it weedy. It is against these population attributes that any agent impact must ultimately be evaluated. Spectacular attack rates alone may not result in a weed population becoming less problematic. It is common practice in elasticity analyses of demographic models to assess how altering each life history attribute affects population density. It is salient to remember however that a given unit of plant density can vary over many orders of magnitude in biomass, and it is more likely that the weediness of most plants will be closely related to the total biomass of the species per unit area, (i.e., biomass density), canopy cover proportion or similar measures of species abundance. The assessment of parameter sensitivity should therefore be in terms of the ultimate effect of the agents upon the appropriate measure of plant abundance.

The prevalence of "Achilles heels" amongst weed populations in the form of a single, highly sensitive lifestage is equivocal. Indeed, it may be fruitful to investigate the patterns of weed attack by control agents considered to be singly responsible for bringing the weeds under control, to gauge whether the agents are primarily influencing a single lifestage transition, or whether they are directly influencing several lifestage transitions. In the cases where several agents were necessary to bring a weed under control, it is clear that an "Achilles heel" was not present. By analysing a weed population model it is possible to compare the lifestage transitions that are influential on population dynamics with the list of putative control agents or species guilds to design a robust, parsimonious system (McEvoy & Coombs, 1999). To achieve a robust system it may often be the case that biological control of the weed will not be sufficient, and cultural control techniques may be necessary to achieve satisfactory results.

In selecting agents for biological control, it is crucial to remember that many weed issues are being tackled in the context of an active invasion. This means that the interrelated population processes that maintain a population's potential for local regeneration and those that fuel invasion potential are distinguished and the interrelationships understood. For example, seeds can create a seedbank from which a population can regenerate following a disturbance. In many cases the seedbanks surrounding exotic weeds become seed-saturated, and recruitment following disturbance becomes heavily constrained by density-dependent mortality processes. Attempts to reduce the local weed population by reducing seed production or attacking seed in the soil seedbank may be futile, or at least very difficult to achieve satisfactory results (Hoffmann & Moran, 1991; Kriticos *et al.*, 1999). Depending upon the relationship between local seed production rates and effective seed dispersal rates however, the reduction of local seed production rates may strongly influence the rate of weed invasion (Hoffmann & Moran, 1991; Isaacson *et al.*, 1996).

Potential distribution

A key component of agent impact is the potential distribution of the agent *vis-à-vis* the potential distribution of the target weed. This defines the proportion of the range of the weed that may be controlled by the agent. A good example of this was the work of Julien, Skarrat and Maywald (1995) comparing the potential ranges of alligator weed, *Alternanthera philoxeroides*, and its biological control agent *Agasicles hygrophila*. This model identified areas where the weevil would have some impact upon the weed, and those areas where additional control efforts would be necessary.

To quantify the potential benefits, a potentially useful economic model could be developed using a climate model such as CLIMEX (Sutherst & Maywald, 1985; Sutherst *et al.*, 1999) for the control agent and the target weed and a suitable economic damage function for the weed.

Climate models of the potential distribution of agents can also be used to highlight areas in which agents should be released based upon the predicted climatic suitability. This would allow re-distribution programs to be conducted more efficiently by initially releasing agents into climatically suitable areas, and subsequently expanding the distribution of potential invasion foci for the control agent.

Boundary zones of agent-weed distribution underlap (i.e., where the weed distribution exceeds the predicted potential distribution of the weed) provide ideal conditions to validate climate models. Monitoring agent releases in these zones would provide information with which to gauge whether the range limitation at that location was correctly predicted in climatic terms. Such information would contribute greatly to the science of predicting potential geographical ranges.

Phenological synchronisation

When considering translocation of organisms across geographic barriers, it is often the case that novel climatic conditions are encountered. For example, the temperature range may be similar, but the seasonal pattern of rainfall may be different. Evaluating the differential effect that this may have on the population dynamics of the agent and the target weed can only be explored using ecological models. Relatively simple development models could, for example, indicate climatic limitation of voltinism, and climatic regions where asynchrony between the plant and the agent either limits agent impact or is prohibitive to agent establishment.

Defining post-release agent impact

There have been few spectacular successes in weed biological control such as water hyacinth, (*Eichhornia crassipes*), where the impact of the agent is so clear that it is unnecessary to undertake more than a cursory analysis in order to gauge the success of the introduction. It is more usually the case that the impact of an agent on a weed requires some form of experimental observation or manipulation in order to evaluate the impact (McClay, 1995). This is particularly so when the effect of the agent is confounded by factors such as interspecific plant competition (Sheppard, 1996), or when multiple agents are involved such as when *Cactoblastis cactorum* and several pathogens were coincidently introduced to control prickly pear *Opuntia* spp. (Mann, 1970). Ecological models such as the inverse-linear model can be used to provide an analytical framework for designing appropriate experiments and correctly interpreting their results (Pantone *et al.*, 1989; Van *et al*., 1998). Population models (especially process-based ones) can then be used to scale these findings up to the level at which the ultimate value of the agent can be interpreted (McEvoy & Coombs, 1999). This valuation process can include a loose-coupling of the population model to an economic analysis such as was done with *Echium plantagineum* by (Nordblom *et al*., 2001).

Ideally, prior to its introduction, an agent's potential impact would be demonstrated in the native range of the weed, or in another, comparable environment into which it has been introduced (Pantone *et al*., 1989). This is however, usually not the case; most agents are introduced and released without effective baseline measurements of the weeds population dynamics even in the target country, prior to the introduction of the agent (McFadyen, 1998). In this context, "effective" means in a form that is suitable for the construction of a model that can control for effects such as plant competition, disturbance and climate. Under such circumstances, ecological models can be used in conjunction with agent exclosure experiments to undertake a retrospective comparison between current post-release and pre-release weed abundance and dynamics.

Discussion and conclusion

The potential role of models in biological control is far more extensive than is commonly practiced (Table 1).

Common rejoinders to suggestions that ecological studies of the weed should be undertaken prior to the introduction of agents are that it costs too much, and that it takes away from the main objective of the exercise which is to import agents. Analyses such as Myers (1985) and Denoth *et al.* (2002) underline the fact that most agents that have been imported have been redundant. The costs of importing each agent is considerable (3 scientist-years, according to McFadyen, 1998) and processes which can reduce the redundancy should be attractive. Whilst it may be difficult to predict successful agents using ecological models and giving due consideration to both plant and insect ecologies and the effects of other disturbances, it is hardly surprising that results have not been better when models have not been used, and when the ecology of the plant has received such scant attention. The costs of processing even one agent should be sufficient to underwrite the ecological studies and model development.

At present, classical weed biological control practice is primarily conducted as an applied entomology or applied pathology project. Primary responsibility for prioritising agents for import and testing is left with the scientist who conducted the field search for agents. In order to now make significant advances, classical biological control must evolve into an inter-disciplinary activity involving *inter alia* plant ecologists and ecological modellers throughout the project lifecycle. The sooner the factors regulating the weed population are understood, the better placed we will be to make better judgements as to what characteristics a successful agent should have, and the better placed we will be to prioritise agents for processing.

It is perhaps axiomatic that biological control scientists have tended to look for evidence of agent impact by focussing their attention on the agent they have introduced. The collection of evidence of impact starts logically enough with agent establishment and persistence. More detailed investigations include attack rates and other proximal effects of the agents at the individual plant level. In very few cases are rigorous experiments to quantify agent impact undertaken (McClay, 1995), and fewer still scale this up to the plant population level (McFadyen, 1998) c.f. (Hoffmann, 1990; Lonsdale *et al.* 1995; Rees & Paynter, 1997; Shea & Kelly, 1998).

References

Blossey, B. (1995) A Comparison of Various Approaches for Evaluating Potential Biological Control Agents using Insects on *Lythrum salicaria. Biological Control* **5**, 113-122.

Crawley, M.J. (1986) The population biology of invaders. *Philosophical Transactions of the Royal Society of London Series B* **314**, 711-731.

Crawley, M.J. (1989) The successes and failures of weed biocontrol using insects. *Biocontrol News and Information* **10**, 213-223.

Denoth, M., Frid, L. & Myers, J. (2002) Multiple agents in biological control: Improving the odds? *Biological Control* **24**, 20-30.

Godfray, H.C.J. & Waage, J.K. (1991) Predictive modelling in biological control: The mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *Journal of Applied Ecology* **28**, 434-453.

Goeden, R.D. (1983) Critique and revision of Harris scoring system for selection of insect agents for biological control of weeds. *Protection Ecology* **5**, 287-301.

Harris, P. (1973) The selection of effective agents for the biological control of weeds. *Canadian Entomologist* **105**, 1495-1503.

Hoffmann, J.H. (1990) Interactions between three weevil species in the biocontrol of *Sesbania punicea* (Fabaceae): the role of simulation models in evaluation. *Agriculture, Ecosystems and Environment* **32**, 77-87.

Hoffmann, J.H. & Moran, V.C. (1991) Biocontrol of a perennial legume, *Sesbania punicia*, using a florivorous weevil, *Trichapion lativentre*: weed population dynamics with a scarcity of seeds. *Oecologia* **88**, 574-574.

Isaacson, D.L., Sharratt, D.B. & Coombs, E.M. (1996) Biological control in the management and spread of invasive weed species. *Proceedings of the IX International symposium on Biological Control of Weeds* (eds V.C. Moran & J.H. Hoffmann), pp. 19-26. University of Cape Town.

Julien, M.H., Skarratt, B. & Maywald, G.F. (1995) Potential geographical distribution of Alligator Weed and its biological control by *Agasicles hygrophila. Journal of Aquatic Plant Management* **33**, 55-60 .

Kriticos, D.J., Brown, J.R., Radford, I.D. & Nicholas, M. (1999) Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control* **16**, 230-239.

Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995) Biological control of a tropical weed: a population model and experiment for *Sida acuta. Journal of Applied Ecology* **32**, 391-399.

Louda, S.M., Kendall, D., Connor, J. & Simberloff, D. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science* **277**, 1088-1090.

Mann, J. (1970) *Cacti naturalised in Australia and their control*. Department of Lands, Brisbane.

McClay, A.S. (1995) Beyond "Before and After:" Experimental Design and Evaluation in classical weed biological control. *Proceedings of the Eighth International Symposium on Biological Control of Weeds* (eds E.S. Delfosse & R.R. Scott), pp. 213-219. DSIR/CSIRO, Melbourne.

McEvoy, P.B. & Coombs, E.M. (1999) Biological control of plant invaders: Regional patterns, field experiments, and structured population models. *Ecological Applications* **9**, 387-401.

McFadyen, R.E.C. (1998) Biological control of weeds. *Annual Review of Entomology* **43**, 369-393.

Myers, J.H. (1985) How many insects are necessary for successful biocontrol of weeds? *Proceedings of the sixth international symposium on biological control of weeds* (ed E.S. Delfosse), pp. 77-82. Agriculture Canada, Ottawa, Ontario.

Nordblom, T., Smyth, M., Swirepik, A., Sheppard, A. & Briese, D. (2001) Benefit-cost analysis for biological control of Echium weed species (Paterson's curse / Salvation Jane). *The CRC for Weed Management Systems: An impact assessment* (ed Centre for International Economics) CRC Weed Management Systems, Waite Campus, University of Adelaide.

Pantone, D.J., Williams, W.A. & Maggenti, A.R. (1989) An alternative approach for evaluating the efficacy of potential biocontrol agents of weeds. 1 Inverse Linear Model. *Weed Science* **37**, 771-777.

Rees, M. & Paynter, Q. (1997) Biological control of Scotch Broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology* **34**, 1203-1221.

Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* **8**, 824-832.

Sheppard, A.W. (1996) The interaction between natural enemies and interspecific plant competition in the control of invasive pasture weeds. *Proceedings of the IX International symposium on Biological Control of Weeds* (eds V.C. Moran & J.H. Hoffmann), pp. 47-53. University of Cape Town.

Simberloff, D. & Stiling, P. (1996) How Risky is Biological Control? *Ecology* **77**, 1965-1974.

Sutherst, R.W. & Maywald, G.F. (1985) A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment* **13**, 281-299.

Sutherst, R.W., Maywald, G.F., Yonow, T. & Stevens, P.M. (1999) CLIMEX: *Predicting the effects of climate on plants and animals. User Guide*. CSIRO Publishing, Melbourne.

Van, T.K., Wheeler, G.S. & Center, T.D. (1998) Competitive interactions between hydrilla (*Hydrilla verticillata*) and vallisneria (*Vallisneria americana*) as influenced by insect herbivory. *Biological Control* **11**, 185-192.

Wapshere, A.J. (1985) Effectiveness of biological control agents for weeds: Present quandaries. *Agriculture, Ecosystems and Environment* **13**, 261-280.

Withers, T.M., Barton Browne, L. & Stanley, J. (2000) *Host-Specificity Testing in Australasia: Towards Improved Assays for Biological Control*. Scientific Publishing, Indooroopilly.

Putting biological reality into economic assessments of biocontrol

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Summary

Prioritising, exploring, identifying and multi-stage screening of potential biocontrol agents is an arduous, sequential attrition process of discovering biological reality against exacting standards. In this it is like gold mining in which tons of rock must be excavated to find an ounce of the precious metal. It may also be compared with musical composition in which many ideas are tried before a piece emerges as an enduring hit. The industry and artistry to produce gold and musical masterpieces are private initiatives that entail both great risks and great rewards. The scientific organization and skill marshalled for research and development of classical biological control entail similar risks but have typically produced public-good benefits far in excess of costs. *Ex ante* analyses, considering potential economic, social and environmental benefits and costs, to sort out priorities for research, are as important as *ex post* studies of completed successful biocontrol projects. In *ex-ante* analyses, damages caused and threatened by a pest in its introduced environment may be clear, while the biological realities of potential biocontrol agents are as yet unknown; scenario testing with different levels of biocontrol efficacy and timing may help identify performance targets for project success. In the case of completed successful projects, the biological realities of both the pest and the agents are often clear enough for confident *ex post* analysis. Examples of economic analyses at different stages of completeness in the knowledge of biological reality of the agents are reviewed. Two insect biocontrol examples use economic methods applicable also to weeds.

Key words: ex ante, ex post, confidence, biocontrol, public-good investment

Introduction

The aim of this paper is to consider ways to improve economic assessments of biocontrol by using the most realistic assumptions regarding the biological factors involved, and placing these correctly in their socio-economic settings. It is also about increases in the level of confidence one may have regarding the biological factors as a project moves from its earliest stages to its mature stages, when the efficacy and specificity of agents have been measured in the introduced range of the target pest. The paper is less about the social and economic factors affecting research and implementation of biological control; on the latter subject one could do no better than see Tisdell *et al.* (1984), Harley & Forno (1992), Auld (1998), Perkins & Garcia (1999), Perrings *et al.* (2000).

An economic analyst, even when teamed with knowledgeable biologists, may be confronted with a difficult (or impossible) task of preparing a confident assessment of the benefits and costs of a proposed biological control program distributed over space and time. This is not because knowledgeable biologists are dishonest, but because the more honest they are, the more they will have to grant how little may be known about key factors required for such an analysis. These key points are outlined below:

Geographically-specific distributions of the target weed, and damages caused by it

If the weed is spreading, projections are needed for its expanding geographic incidence and damages over time. An important aspect is the range of climatic zones, land classes and land uses in which the weed is problematic, i.e., in crops, pastures, native vegetation or aquatic environments. Thus, both the ecological and economic characteristics of the weed's geographic distribution are critical points. Estimates of the damages due to the weed may be influenced by its interference with land uses and the environment.

Ecologically-specific characteristics of the bio-control agent

With biological control, rapid, complete and sustained relief of damages is rarely (or never) expected. The question then becomes one of specifying rates of biocontrol agent spread, development of effective densities, and effects upon the target weed in the various environments. The pace and the degree of relief of damages following a release of biocontrol agents in each environment will need to be expressed among the assumptions of the economic assessment.

Horse-and-rabbit stew

Mishan (1976) characterised cost-benefit analysis (CBA) as “horse-and-rabbit stew”, in which the ratio is always one rabbit to one horse. The rabbit represents costs and benefits that really can be quantified, and the horse represents other considerations, including environmental and social spill overs, that are difficult to confidently quantify. Mishan concluded that economists must resist the temptation to ignore the horse, because: “No matter how carefully the scientific rabbit is chosen, the flavour of the resulting stew is sure to be swamped by the horse flesh.” (The Hastings Center, 1980). Often it is not possible to fully quantify likely social and environmental costs and benefits associated with a biocontrol program. However, taking the effort to describe such costs and benefits qualitatively can lend the advantage of broader perspectives for evaluation of agricultural research and extension measures (Hill & Greathead, 2000).

The ‘counterfactual’

Marshall & Brennan (2001) have noted the importance of accounting adequately for the “without project” scenario in any benefit-cost analysis. Where the analysis is *ex ante* (before the fact), or prior to a biocontrol project, it will require projections of future losses **without** the project as well as projections of reductions in these losses **with** the project. What will (would have) happen(ed) without the project? Consider a case in which an entire industry (say canola or food-legume production) is threatened in an area by a weed (say wild radish or broom rape, respectively). If there is still a possibility to grow other crops, even if less profitable than the former, the benefits so gained would reduce the losses otherwise attributable to the pest. Thus, the value of the next-best option must be considered in calculation of the losses due to a pest in a particular crop or system. At an early stage in a biocontrol process several scenarios of cost and benefit streams over time may be projected for different contingencies, with and without the project, with different subjective probabilities assigned to each. In a retrospective study of a mature biocontrol project, a realistic “counterfactual” (without-project) scenario is still very much needed in order to calculate the difference in benefits and costs due to the project’s existence.

Lower equilibrium density

Another reason the potential benefit of biocontrol may be less than the total value of the losses caused by the pest is that the target pest is never driven to extinction, except in local patches, but only reduced to some lower density in fluctuating equilibrium with the agents. With luck, the new equilibrium density of the pest may fall to a level causing negligible damage. In other cases it may still cause some or significant economic damage in some locations. While it is obvious that benefits are limited to the part (or fraction) of the problem that can actually be ameliorated (McInerney, 1996), the precise degree of success in biocontrol cannot be known in advance.

Collateral damage

Important also are costs that could arise due to lack of specificity of biocontrol agents introduced to a new range, though the chances of this happening may be reduced to near zero through appropriate screening and specificity testing. One of the worst examples of things going wrong is the cane toad, introduced against the advice of scientists, in the unfounded belief that the toad would control insects in sugar cane fields. It has instead spread widely in the environment, destroying native fauna. We may never assume in advance of rigorous specificity testing that a potential agent will not harm crops, pastures, or any other part of the environment, from endangered species to ornamental plants. Where ‘collateral damage’ is determined to be a risk with introduction of an agent, such costs need to be taken into serious consideration.

Resolution of unknowns

A theme developed in this paper is the gradual resolution of the unknowns over the course of a biocontrol research and development program, with subsequent improvement in the confidence possible in economic analyses. Later in the paper, examples are given of economic evaluations of projects at different stages of completeness. Evaluations made at the earliest stages must fill in the unknown parameters with assumptions. For biocontrol projects in the mature stages, however, sufficient scientific monitoring and reporting of agent behaviour and pest response in the field may be available to allow confident *ex post* (after the fact) economic evaluation. Few, if any, parameters can be known with absolute certainty, particularly in advance of implementation of a biological control program and careful monitoring of its consequences. Nevertheless, biologists are often able and/or willing to make reasoned guesses on some or all the parameters. Things could be worse: the guesses could be left for the economic analyst to make on his/her own.

The uncertainties that may gradually be resolved over the course of developing a biocontrol program for a weed would include the following:

- Is the target weed causing significant economic, environmental, health or amenity damages in its introduced range?
- Is the weed spreading and threatening wider damages beyond its present introduced range? Quantitative estimates of rates of spread, probable ultimate limits to the introduced range, and time paths to these, are useful.
- Are there biological agents that limit the weed in its native range?
- Are these agents specific to the weed and significantly limiting it in its native range?
- Are the agents specific to the weed while posing no threat in the environment of the introduced range of the weed, nor to present or future agricultural options or to ornamental plants?
- How can the agents be reared, released and established successfully in the introduced range of the weed?
- Are the agents able to establish on the weed and limit it in the introduced range?
- Are the agents able to increase their populations and spread to the weed throughout its introduced range without redistribution programs?
- What are the costs and effectiveness of agent redistribution programs?
- What are the paces of spread and effective attack of agents on the weed in different environments of the introduced range?
- How complete is the degree of control of the weed's damage in different parts of its introduced range?
- What takes the place of the weed when it is limited by agents… useful plants or other weeds?

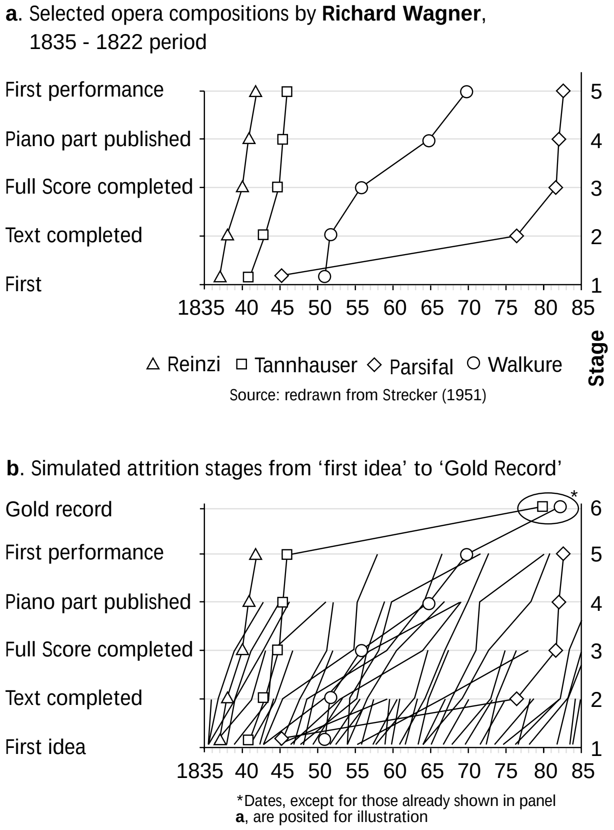
The above (non-exhaustive) list illustrates a number of points of biological reality which may stand as 'unknowns' at the outset of a biocontrol program but become known with considerable confidence in the final stages. In the case of a weed for which biocontrol research hits an early obstacle, such as lack of specificity or efficacy in any of the potential agents, the questions later in the list are mooted as agents drop from consideration. In other cases, an obstacle may arise later in the process, for example, where it is found that none of the agents are able to establish and prosper upon release in the introduced range of the weed.

Stages of biocontrol research and development

When classical biological control is successful, it has ususally been achieved through a number of stages: (1) recognition that an exotic pest may be a candidate for biocontrol, particularly when it is known to be more subdued in its native range than its introduced range; (2) exploration of the pest's native range for agents attacking it, and research on the specificity of attack on the pest; (3) successful application for importation of agent into quarantine; (4) testing in quarantine for specificity of the agent to the pest, efficacy against the pest, safety for crops and other species, particularly natives, and experimentation to find most effective rearing technique; (5) after approval of specificity and efficacy criteria, first field test releases of agent against the pest, close monitoring of spread and efficacy, establishment of agents, and an expanded program of releases; and (6) widespread control of the pest.

Such a sequence of steps in developing a successful biological control program for a particular weed may be compared to that describing the history of some of the great works of music. The inspiration for this is Strecker's (1951) time-chart of the development of Richard Wagner's operas over the period from 1835 to 1882. The chart defines five stages: (1) the first idea; (2) text completed; (3) full score completed; (4) piano part published; and (5) first performance. Four years was Wagner's shortest span from first idea for an opera to its first performance (*Tannhäuser*), and 37 years was his longest (*Parsifal*). More representative of Wagner's time in over-lapping completion of 11 major operas was his ever-popular *Walküre* (Ride of the Valkyries), 19 years all together! (Figure 1a). Only the evolutions of Wagner's most famous operas to the date of their first performances were traced in Strecker's chart.

If we add a sixth stage in music, "popular acclaim and expanded demand for repeat performances", equivalent perhaps to "Gold record" status, the time-spans and stages are not unlike those of successful biological control projects. As is surely the case with the first sketches of musical compositions, many biological control prospects do not survive beyond the first or second stage (Figure 1b), while others drop out in the intermediate stages of screening. We may envisage a side-by-side listing of the six stages of musical development and biological control efforts with different levels of attrition between stages (Figure 2). One may imagine ten operas that reach the stage of first performance, of which only two become popular hits (Figuref 1b). Likewise, our example has two of ten agents that reach the stage of release in the field and go on not only to establish and spread, but to achieve widespread limitation of the weed. This obviously takes place in the context of a much larger process of attrition.


a. Selected opera compositions by **Richard Wagner**, 1835 - 1822 period

Source: redrawn from Strecker (1951)

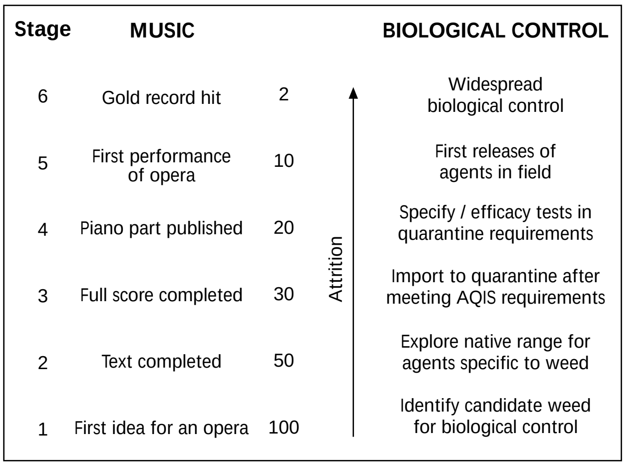
b. Simulated attrition stages from ‘first idea’ to ‘Gold Record’

*Dates, except for those already shown in panel **a**, are posited for illustration

Figure 1. Stages and attrition in musical development from first idea to hit record sales.

Syrett *et al.* (2000) make the case that some studies have understated the success of biological control introductions by virtue of assessing them too early, citing McFadyen (1998), “before agents have had a chance to achieve their full potential, and … partial successes have often been counted as failures.” Van Lenteren (1995), citing Hall & Ehler (1979), reported that only some 40% of 2295 organisms introduced for biological control of insects became established, with only about a quarter of these becoming widespread and, citing Crawley (1986), that 65% of 627 organisms introduced against weeds became established, with half of these becoming widespread. This is the sort of attrition one could expect between the number of projects that reach stage 5 (field releases) and the number reaching stage 6 (widespread limitation of the target pest).

In a description covering the whole range of biocontrol research stages Cullen & Whitten (1995) paraphrased Marsden *et al.* (1980): “…the majority of projects were ‘dry holes’ in that they yielded negligible economic return, but that it only needed one or two successes to pay for the entire operation of a large research agency over a decade or more…. Less than half of biological control projects produce substantial returns, but those that do are the really big winners.”



Stage	MUSIC		BIOLOGICAL CONTROL
6	Gold record hit	2	Widespread biological control
5	First performance of opera	10	First releases of agents in field
4	Piano part published	20	Specify / efficacy tests in quarantine requirements
3	Full score completed	30	Import to quarantine after meeting AQIS requirements
2	Text completed	50	Explore native range for agents specific to weed
1	First idea for an opera	100	Identify candidate weed for biological control

Figure 2. Attrition between stages of musical and biological control efforts.

Scans of the literature, which are increasingly fast and rich, help provide the basis for stage 1 in which a problematic exotic weed is shown to host possible biocontrol agents in its native range. An economic study done at this stage may be able to roughly estimate the damages caused by the weed and potential future damages should the weed spread to various extents beyond its current introduced range. The degree of confidence in biological reality supporting such an early analysis will necessarily be low. Nobody can know if any of the potential agents will be effective in the introduced range. The fullest confidence will typically be possible only after several further stages of research and development.

Essential research into agent identification, specificity and efficacy on the host, effective rearing and release methods, and geographic spread and attack rates in the field, comprises the discovery of successive stages of biological reality.

Examples

Legner (2002) has reviewed a number of studies with the aim of emphasising the economic and other advantages of biocontrol in contrast to chemical methods. Gutierrez *et al.* (1999) have summarised results of economic analyses from 23 classical biological control programs around the world with starting dates from 1905 to 1978 and benefit: cost ratios ranging from 14 to 12,698. A slightly overlapping list of 27 *ex post* economic assessments of biocontrol programs published from 1955 to 1990 is offered by Hill & Greathead (2000) in which benefit: cost ratios ranged from 0.99 to 7,405. Many of the highest-benefit programs saved industries from collapse using only modest biological control research and development funds. The discounted value of the particular industry losses avoided (or proportions thereof distributed over a time sequence), divided by the cost of the program, provided the rough method by which some of these benefit: cost ratios were derived. Others among the list were done more rigorously by professional economists. It is possible to place a number of economic assessments of biological control programs in our scale of 1 to 6.

Old man's beard

Greer & Sheppard's (1990) study contacted all council-level noxious weeds authorities in New Zealand for estimates of conventional control costs expended on *Clematis vitalba*, a climbing vine that smothers and kills native trees. With a 10% discount rate, the present value of such costs continuing indefinitely in the future was estimated at around NZ$900,000. The authors also conducted a mail survey of a random sample of 3000 residents (names and addresses drawn from electoral polls) across the country to derive a distribution of 'contingent valuations" of their "willingness-to-pay" for a biocontrol research program. Though respondents had been advised that favourable biocontrol research results were highly uncertain, the mean estimate of consumer surplus attributed to such a research program was NZ$46.37. Multiplying this by the population sampled, the number of New Zealanders over 18 years of age gave an "estimated aggregate consumer surplus from research into control of *Clematis vitalba*" of NZ$111 million. In this case, though, no biocontrol agents were known for the pest at the time. The 'biological reality' was that the weed was seen to pose a considerable environmental threat by spreading to native trees in inaccessible areas and that eradication by pulling up plants and chemical sprays had not been shown to work. Thus, the authors concluded the "allocation of research funds to the biological control of *Clematis vitalba* is fully justified." This promotion to candidacy placed the program at the beginning of stage 1 of our scale from 1 to 6.

Hawkweed

A second example represents the middle of stage 1 in which a weed is identified as a candidate for biocontrol. "Most herbicides" would not control it, it was widespread and particularly problematic in inaccessible sites and a number of potential agents had been identified in the plant's native environment, Europe, where it is not seen as a significant weed problem (Grundy, 1989a). This is the case of *Hieracium* spp. on unfertilised or poor sites in the tussock grasslands of the moderate to low rainfall areas of New Zealand's South Island high country. Judged to be as frequently present as gorse, and continuing to spread, *Hieracium* was estimated to cause annual losses to the country on the order of NZ$1.1 to 4.4 million in terms of lost grazing.

Twenty two years later, Parsons & Cuthbertson (2001) noted that *Hieracium* spp. has recently been added to the noxious weeds list of New South Wales. Rudman & Goninon (2002) reported an eradication case history on *Hieracium pilosella* in Tasmania, where the state's 'weed incursion response plan' was initiated, including an assessment of the potential impact of this weed, after a small naturalised population was found on agricultural land in January 2001. In this case, "fortunately, eradication was easily facilitated within the road-widening works proposed for the area… at little extra cost."… "The operation involved scalping the soil (top 15 cm) from the infested area and a substantial buffer area and deep burying the material on site. The area scalped has been subsequently buried beneath the road works…" Such timely and thorough eradication of a pest incursion will rarely be possible. This is most likely not the end of the matter as Rudman & Goninon (2002) expect further incursions and naturalisations of *Hieracium* to occur.

Grundy (1989a) pointed out that *Hieracium* is controllable on good pasture lands in New Zealand by fertilisation and establishment of pasture species. However, on poorer lands and inaccessible areas, control by such pasture development measures was not feasible. That parts of Tasmania are similar in character to the worst infested areas in New Zealand was considered in the risk assessment by Rudman & Goninon (2002), justifying the timely eradication effort. Considered at stake in Tasmania, beyond the potential loss of grazing value, was loss of biodiversity in grassland communities, which contained "nine nationally listed threatened species and a further 30 State-listed threatened species." Importantly, "many of these threatened species occur in the inter-tussock spaces that *H. pilosella* so successfully dominates in New Zealand grasslands."

Because no sound basis existed for estimating the ultimate effectiveness of a biocontrol program on *Hieracium*, while a research program would most certainly cost something on the order of NZ$1 million, Grundy (1989a) advised caution toward such an investment. Perhaps now, as increasing potential losses from this pest are recognised, and more may be known regarding the chances of successful biocontrol, further research support toward that end is justified. The prevention of new incursions and detection and eradication of any new populations looks to be the best strategy in the mean time for regions that are still uninfested (Rudman & Goninon, 2002). Biocontrol of *Hieracium* may be between stages 1 and 2.

Sweet briar

Grundy (1989b) also completed an economic analysis on the economics of biocontrol of sweet briar (*Rosa rubiginosa*) which "is present on over 400,000 hectares in the South Island." The annual expenditure on chemical control of this pest was estimated at NZ$600,000 and the continuing opportunity cost in reduced pasture productivity at NZ$2 to 4 million. Grundy (1989b) noted that several potential biocontrol agents had been identified, but at that time none had been introduced. This placed sweet briar between stages 2 and 3 at that time.

Twelve years later, Parsons & Cuthbertson (2001) suggested sweet briar was responsible for losses of grazing capacity on the order of 1.1 million ewe equivalents in New Zealand and, while agents have been identified, they also attack ornamental roses. For the moment, this would seem to block the biocontrol program at stage 4. Unless sweet briar agents can be controlled on ornamental roses along with other insect pests or new agents can be identified, this may be the final stage.

Paterson's curse

Echium plantagineum is an introduced winter annual weed of Mediterranean origin. Free of its native plant and insect communities it has become an important pasture weed of temperate Australia. Although relatively nutritious in terms of digestible protein, *Echium* contains pyrrolizidine alkaloids poisonous to livestock, reducing weight gain and wool clip and, in severe cases, leading to death. In 1985, *Echium* was estimated to cover 33 million hectares (IAC Report, 1985). First suggested as a candidate for biological control at the Australian Weeds Council in 1971, *Echium* became the subject of surveys begun in 1972 in its native range by CSIRO Entomology from its base in Montpellier, France. Of the hundred or more insect species recorded on *Echium*, eight were selected as possible biological control agents, with the first imported into quarantine, Canberra, by 1979. In 1980, two graziers and two apiarists lodged an injunction in the Supreme Court of South Australia to stop the biological control program as they considered the loss of *Echium* a threat to their livelihood. The Biological Control Act (1984) established procedures for assessing and authorising biological control programs in Australia; a subsequent inquiry and benefit-cost analysis was conducted by the IAC, which concluded with the judgement that a biological control program on *Echium* should go ahead (IAC Report, 1985). Later studies (Sloane, Cook & King, 1989; Tisdell, 1990) instructively criticised some of the assumptions and methods of the IAC report (1985), but supported its conclusions.

The Supreme Court injunction was finally lifted at the end of 1988 and the importation of insects into Australia resumed. Since then, six insect species were successfully released. Of these a leaf mining moth, *Dialectica scalariella*, and a crown weevil, *Mogulones larvatus*, were introduced first and have been released across the geographic range of the weed. *M. larvatus* is limiting the weed population at two of the earliest release sites and approaching control at many of the younger release sites (Sheppard *et al.*, 1999).

Based on the positive population trend of *M. larvatus* and its ability to limit the weed at an increasing number of sites, the economic analysis of the IAC report was revisited so projected gains could be up-dated based on the release program begun in 1993 (Nordblom *et al*., 2001), attaining 400 successful releases (populations established by 2000). Unlike some cost-benefit analyses of biological control, where an insect is given an arbitrary impact and rate of spread, the analysis incorporated observed values based on the biology and ecology of *M. larvatus* and its weedy host over the last 9 years. The new analysis used data on incidence and damage from the IAC (1985) report with a gradual partial relief of pasture productivity losses according to elapsed time from numbers of releases in particular districts, based on CSIRO and state collaborators' observations. Each district has unique climate, size, weed infestation and pasture productivity values; insect spread and attack density rates were defined as functions of time with parameters specific to each of three climates (months of opening rains) (Nordblom *et al.*, 2001).

The success story projected for biological control of *Echium* in Australia will likely be at a slower pace than envisaged by the IAC report of 1985. Nevertheless, the return on investments is expected to be very respectable. Annual benefits in terms of increased productivity of grazing lands are projected to increase from near-zero in 2000 to some $73 million by 2015. The discounted (5%) net present value (NPV) of the benefit-cost stream from 1972 to 2015 is projected at $259 million, for a benefit: cost ratio of 14.1:1 and yielding an internal rate of return exceeding 17%. Because lower attack and spread rates of the insects are observed in regions with late autumn opening rains, a slow build-up of benefits is expected to continue over many years. The discounted NPV for the 1972-2050 period is estimated to be $916 million, with a benefit: cost ratio of 47.5:1 and an internal rate of return above 19%. These estimates do not explicitly take into account reductions in costs of current *Echium* control measures that are expected with the successful spread of the biocontrol agents. Land managers (graziers) will have to make some changes in grazing and spraying practices in order to help the success of the biocontrol agents. To the extent that these changes are not costless, they will tend to balance somewhat the benefits from reduced control costs (Nordblom *et al.*, 2001, 2002a, b).

A question remained about whether further releases of insects against *Echium* might be justified and, if so, where and how many. A new analysis focussing on these questions indicates good returns on investment are available if further releases are targeted to districts with relatively few prior releases and large remaining potential gains in recovered pasture productivity (Nordblom *et al.*, 2002c). This study took into account the expected continued expansion of insect populations from the prior release program and focussed on the potential to speed up the process with new releases. The slowness of spread and attack rates observed in the insects released against *Echium*, with or without new releases, means most of the benefits of this biocontrol program are still in the future. This places the program between stages 5 and 6, as the full benefits of field releases begun only over the past decade have not yet been realised.

Tansy ragwort

Coombs *et al.* (1996, 2000) describe a successful, mature biocontrol project for *Senecio jacobaea L*. in Oregon, yielding a 15:1 benefit:cost ratio. That project began in 1960 and by the early 1990’s had shown widespread effectiveness. First recorded in western Oregon in the early 1900s, tansy ragwort became a serious weed, occurring on an estimated nine million ha. Cattle and horses are vulnerable to poisoning by the pyrrolyzidine alkaloids present in the plant and such losses were estimated in the range of US$1.5 million to US$10 million annually. Smaller infestations have spread to eastern Oregon.

The cinnabar moth (*Tyria jacobaeae L.*) was successfully introduced to Oregon in 1960. A concerted state and county redistribution program from 1974 to the end of the decade, releasing some five million larvae, resulted in establishment of about 5000 colonies of insects on the weed across most of the ragwort-infested areas of western Oregon (Isaacson, 1978; Hawkes, 1981). In 1971, a second biocontrol agent, the flea beetle (*Longitarsus jacobaeae*) was introduced, followed in 1976 by the ragwort seed fly (*Pegohylemyia seneciella*) (Coombs *et al.*, 1995). In terms of savings due to reduced livestock poisoning, increased pasture production and reduced herbicide use, benefits of the tansy biocontrol program in western Oregon are about US$5 million annually (Radtke, 1993; Coombs *et al.*, 1996). Radtke’s (1993) analysis of the economic benefits and costs of tansy biocontrol in Oregon is rare in that it is a retrospective *(ex post*) view of a program proven to be widely successful and on which good measures of effectiveness were available. It is at stage 6 in Oregon.

Ireson *et al.* (1999) describe the biological control effort on tansy ragwort in Tasmania, with agents in the ‘field release and establishment’ stage (5). These had not yet reached the stage of widespread limitation of the weed.

Insect agents against insect pests

Banana skipper

A recent example of an insect agent controlling an insect pest has been described in a study that calculated Australia would suffer ‘without project’ losses having a present value of A$223m if not for an ACIAR biological control project in Papua New Guinea where benefits were valued at an additional A$201m (Waterhouse *et al.*, 1998). The ACIAR project is judged to have contained and minimised the effects of an early 1980’s invasion of the ‘banana skipper’ butterfly (*Erionota thrax*), a damaging pest of banana production capable of infesting new areas at a rate of 500 km per year. The project is reckoned to have prevented heavy losses in Papua New Guinea and, due to sharply reduced banana skipper densities in that country, markedly lowered the risk of these butterflies invading Australia, whose banana industry is vulnerable. The total present value of benefits to both countries (A$424m) and the present value of ACIAR project costs (A$0.7m), imply a benefit: cost ratio of 607:1. The banana skipper story depicts a biological control program at stage 6.

Cassava mealybug

Gutierrez *et al.* (1999) hailed biological control of the cassava mealybug over the vast cassava belt of Africa as a monumental achievement and asked: “How does one price the reduction or prevention of human misery?” Zeddies *et al.* (2001) have succeeded in capturing the complex economic side of this biological control program across 27 countries, from Angola to Kenya and from Senegal to Zambia. Each country was reckoned to have its total cassava production distributed in percentage terms among its Savannah, Rainforest and Highlands ecological zones. Each of the three ecological zones offered a different environment for the mealybug to establish itself and damage cassava yields, and for the biocontrol agent to overcome the pest and reduce its effects. According to field observations in the three ecological zones, rates of damage onset and biocontrol relief were keyed to the time (in years) since first appearance of the agent in each country. This biological control program by the International Institute for Tropical Agriculture (IITA) and its national and international partners, is estimated to have achieved an economic benefit: cost ratio of about 200:1, even if calculated only through the year 2013 (Zeddies *et al.*, 2001). According to van Driesche & Bellows (1996), the success of cassava mealybug biocontrol has caused international agencies to seriously consider using biological control based on the introduction of new species of natural enemies. Cassava mealybug biocontrol is at stage 6.

Summary

We may set out the examples given above in a way which emphasises the point that economic impact studies may be done at any stage of a biocontrol project (Table 1). Though distributed evenly among these examples, published *ex ante* studies are rarer than *ex post* analyses, probably because the latter are most useful in establishing and confirming the track-record of an institution. The benefit: cost ratios of successful, mature biocontrol projects are often very high. That this is true is due to the number of screenings, tests and hurdles a project must pass before reaching stage 5: field release in the introduced range of the pest.

Discussion

While some biological control programs may have reached beyond one of the intermediary stages (2, 3 or 4) before being terminated due to discovery of some fatal 'biological reality' (non-specificity, low efficacy, failure to establish, etc.), publishing such findings is an essential contribution to science. This makes the science successful as a building block for the future. The maximum degree of confidence anyone can have in the "biological reality" available for an economic analysis will vary from low in the case of *ex ante* studies, before the start of biocontrol work on a weed, to high in the case *ex post* studies, after a project is completed and the effectiveness of agents has been documented. The economic analysis of a biocontrol project can be no more confident than the understanding of the biological reality of progress of the agents in the introduced range of the weed. There is no fixed rate at which uncertainties are dispelled about the success of a particular biocontrol program, from identification of a weed as a potential

Table 1. Examples of economic analyses done at early, intermediate and late stages of biological control projects.

Pest	Common name	Economic study	Stage					
			Candidate pest identified 1[a]	Explore native range 2	Import to quarantine 3	Specificity and efficacy testing 4	Release and establishment 5	Widespread biocontrol 6[p]
Clematis vitalba	Old man's beard, N.Z.	Greer & Sheppard (1990)	✓					
Hieracium spp.	Hawkweed	Grundy (1989a)		→				
Rosa rubiginosa	Sweet briar	Grundy (1989b)			→			
Rosa rubiginosa	Sweet briar	Parsons & Cuthbertson (2001)				✓		
Echium spp.	Paterson's curse	IAC (1985)				✓		
Echium spp.	Paterson's curse	Sloane, Cook & King (1988)				✓		
Echium spp.	Paterson's curse	Nordblom *et al*. (2001, 2002)					✓	
Senecio jacobea	Tansy ragwort, Tas.	Ireson et al. (1999)					✓	
Senecio jacobea	Tansy ragwort, Oregon	Radtke (1993)						✓
Erionota thrax	Banana skipper	Waterhouse *et al.* 1998						✓
Phenacoccus	Cassava mealybug	Zeddies *et al*. (2001)						✓

a *ex ante* "before the fact" studies of prospective, un-proven project ideas

p *ex post* "after the fact" studies of completed, successful projects candidate, through to a completed program ultimately successful in achieving some degree of limitation of the weed.

The following passage is paraphrased from Hill & Greathead (2000): In spite of the high attrition rates from 'first idea' to 'widespread control', biocontrol projects have proved to be a cost-effective use of public funds. Due to the sustainable and self-renewing nature of biocontrol, returns to these programs can be higher than those of other successful agricultural technology research, and significantly higher than average returns on public-good investment programs. *Ex post* studies of completed biocontrol projects have proved to be robust and useful tools, but the greater and largely untapped potential of economic evaluations is in *ex ante* studies, especially those which combine economic and technical *ex ante* analyses of costs and benefits. These would offer decision makers better means of assessing the scope of problems associated with invasive species, of making quicker and better decisions on funding biological control or other agricultural research and extension efforts, and of improving further the returns on investment in biocontrol programs.

Before concluding, I quote Perkins & Garcia (1999): "Biological control, based on modern biological sciences, draws from the mechanistic traditions of modern technological societies but it places the fate of economic activities at the mercy of another species, which is not entirely within human control. This latter quality … may be philosophically alien to researchers, commercially aggressive farmers and regulatory officials. A different world view that allows comfort with reliance on a species not within our complete control may be necessary for enthusiasm about biological control."

I am happy to note that some of those who seem most comfortable relying on other species have developed such broad world views that they are able to go as far as to team up with *economists* to seek research and operational funding in the public interest. And so it should be.

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References

Auld, B.A. (1998) On the social value of biological control of weeds. *International Journal of Social Economics*. Bradford.

Biological Control Act 1984 (1984) Commonwealth Government of Australia. http://scaleplus.law. gov.au

Coombs, E.M., Isaacson, D.L. & Hawkes, R.B. (1995) The status of biological control of weeds in Oregon. *Proc., VIII International Symposium on Biological Control of Weeds*. (eds. Delfosse, E.S. & Scott, R.R.), pp. 463-471, Lincoln University, New Zealand.

Coombs, E.M., Radtke, H., Isaacson, D.L. & Snyder, S.P. (1996) Economic and regional benefits from the biological control of tansy ragwort, *Senecio jacobaea*, in Oregon, In *Proceedings, IX International Symposium on Biological Control of Weeds*. (eds. V.C. Moran and J.H. Hoffmann), pp. 489-494. University of Cape Town, South Africa.

Coombs, E.M., Radtke, H. & Nordblom, T.L. (2000) Economic benefits of classical biological control. In *Abstracts of the III International Weed Science Congress*, p.174. International Weed Science Society, Oregon State University, Corvallis. http://www.olemiss.edu/orgs/iws/wees_abstracts _6-2-00.pdf

Crawley, M.J. (1986) The population biology of invaders. *Philosophical Transactions Royal Society London* B **314**, 711-731.

Cullen, J.M. & Whitten, M.J. (1995) Economics of classical biological control: a research perspective. In *Biological control: benefits and risks* (eds. Hokkanen, H.M.T. & Lynch, J.M.), pp. 270-276. Cambridge University Press.

Greer, G. & Sheppard, R.L. (1990) An economic evaluation of the benefits of research into biological control of *Clematis vitalba*. Research Report No. 203. Agribusiness & Economics Research Unit, Lincoln College, New Zealand.

Grundy, T.P. (1989a) An economic evaluation of biological control of Hieracium. Research Report No. 202. Agribusiness & Economics Research Unit, Lincoln College, New Zealand.

Grundy, T.P. (1989b) An economic evaluation of biological control of sweet brier (*sic*). Research Report No. 201. Agribusiness & Economics Research Unit, Lincoln College, New Zealand.

Gutierrez, A. P., Caltagirone, L. E. & Meikle, W. (1999) Evaluation of Results. In *Handbook of Biological Control: Principles and Applications*. (eds. T. S. Bellows & T.W. Fisher), pp. 243-251. Academic Press, San Diego.

Hall, R.W. & Ehler, L.E. (1979) Rate of establishment of natural enemies in classical biological control. *Bulletin of the Entomological Society America* **25**, 280-282.

Harley, K.L.S. & Forno, I.W. (1992) *Biological control of weeds: a handbook for practitioners and students*.. Inkata Press, Melbourne.

Hawkes, R.B. (1981) Biological control of tansy ragwort in the state of Oregon, U.S.A., *In Proceedings of the Fifth International Symposium on Biological Control of Weeds.* (ed. E.S. Del Fosse), pp. 623-626. CSIRO, Melbourne.

Hill, G. & Greathead, D. (2000) Economic evaluation in classical biological control. *The economics of biological invasions*. (eds. Perrings, C., Williamson, M. & Dalmazzone, S.) pp. 208-223. Edward Elgar, Cheltenham, UK.

Ireson, J.E., Holloway, R.J., Chatterton, W.S. & Leighton, S.M. (1999). An overview of the establishment, distribution and efficacy of biological control agents for ragwort *Senecio jacobaea L.*, in Tasmania. *Proceedings of the 12th Australian Weeds Conference*. (eds. Bishop, A.C., M. Boersma & C.D. Barnes), pp. 425-430. Tasmanian Weed Society, Devonport.

Isaacson, D.L. (1978) The role of biological agents in integrated control of tansy ragwort. *Proceedings of the IV International Symposium on Biological Control of Weeds*. (ed. Freeman, T.J.) pp. 189-192. Gainesville, Florida, USA.

IAC (Industries Assistance Commission) (1985) *Biological control of Echium species (including Paterson's curse / Salvation Jane).* IAC Report No. 371. Australian Government Publishing Service, Canberra.

Legner, E.F. (2002) *Discoveries in Natural History and Exploration*. University of California-Riverside. http://www.faculty.ucr.edu/~legneref/

McFadyen, R.E. (1998) Biological control of weeds. *Annual Review of Entomology* **43**, 369-393.

McInerney, J. (1996) Old economics for new problems - livestock disease: Presidential Address. *Journal of Agricultural Economics* **47**, 295-314.

Marsden, J.S., Martin, G.E., Parham, D.J., Risdill-Smith T.J. & Johnston, B.G. (1980) *Returns on Australian Agricultural Research: the Joint Industries Assistance Commission - CSIRO benefit-cost study of the CSIRO Division of Entomology.* CSIRO, Melbourne.

Marshall, G.R. & Brennan, J.P. (2001) Issues in benefit-cost analysis of agricultural projects. *Australian Journal of Agricultural and Resource Economics* **45**, 195-213.

Mishan, E.J. (1976) *Cost-benefit analysis*. Revised Edition. Praeger. New York.

Nordblom, T., M. Smyth, A. Swirepik, A. Sheppard & D. Briese (2001) Benefit-cost analysis for biological control of *Echium* weed species (Paterson's curse / Salvation Jane). *The CRC for Weed Management Systems: an impact assessment.* Cooperative Research Centre for Australian Weed Management, Technical Series No. 6, pp. 36-43.

——— (2002a) Paterson's curse, a A$100m-a-year weed, faces biocontrol in Australia. *Biocontrol News & Information, 23, CAB International,* http://pest.cabweb.org/Journals/BNI/Bnimain.htm

——— (2002b) Benefit-cost analysis for biological control of Echium spp. (Paterson's curse) in Australia, 1972-2050. *Proceedings of the 13th Australian Weeds Conference*, (eds Spafford Jacob, H., Dodd, J. & Moore, J.H.), pp. 753-756.

——— (2002c). Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agricultural Economics* **27**, 403-424.

Parsons, W.T., Cuthbertson, E.G. (2001) *Noxious weeds of Australia*. Inkata Press, Melbourne.

Perkins, J.H. & Garcia, R. (1999) Social and economic factors affecting research and implementation of biological control. In *Handbook of biological control: principles and applications of biological control.* (eds. T. S. Bellows & T.W. Fisher), pp. 993-1009. Academic Press, San Diego.

Perrings, C., Williamson, M. & Dalmazzone, S. (eds.) (2000) *The economics of biological invasions*. Edward Elgar, Cheltenham, UK.

Radtke, H.D. (1993) An economic evaluation of biological control of tansy ragwort. Oregon Department of Agriculture. State Weed Board. Feb. 1993.

Rudman, T. & Goninon, C. (2002). Eradication case history, *Hieracium pilosella* L. ssp. *nigrescens* (Fr.) Nagel & Peter in Tasmania. In *Proceedings of the 13th Australian Weeds Conference*, (eds Spafford Jacob, H., Dodd, J. & Moore, J.H.) pp. 304-306.

Sheppard, A.W., Smyth, M.J. & Swirepik, A. (1999) Impact of the root-crown weevil (*Mogulones larvatus*) and other biocontrol agents on Paterson's curse in Australia: An update. *Proceedings of the 12th Australian Weeds Conference*, (eds. A.C. Bishop, M. Boersma & C.D. Barnes), pp. 343-346. Tasmanian Weed Society, Devonport.

Sloane, Cook & King Pty Ltd (1989) *The economic impact of pasture weeds, pests & diseases on the Australian wool industry*. The Australian Wool Corporation. Melbourne.

Strecker, L. (1951) *Richard Wagner als Verlagsgefährte.* Mainz. Tabelle III. Cited in Tufte, E.R. (1990) *Envisioning information*. p.111. Graphics Press. Cheshire, Connecticut.

Syrett, P., Briese, D.T. & Hoffmann, J.H. (2000) Success in biological control of terrestrial weeds by arthropods. In *Measures of success in biological control* (eds S.D. Wratten & G. Gurr), pp 189-230. Kluwer, Amsterdam.

Tisdell, C. A. (1990) *Natural resources, growth and development: economics, ecology and resource scarcity*. Praeger. New York.

Tisdell, C.A., Auld, B.A. & Menz, K.M. (1984) On assessing the value of biological control of weeds. *Protection Ecology* **6**, 169-179.

The Hastings Center (1980) *Values, ethics, and CBA in health care*. Institute of Society, Ethics and the Life Sciences. Hastings on Hudson, New York. http://www.wws.princeton.edu/

van Driesche, R.G. & Bellows, T.S. (1996) *Biological control*. Chapman & Hall, New York.

van Lenteren, J.C (1995) Frequency and consequences of insect invasions. In *Biological control: benefits and risks* (eds. H.M.T. Hokkanen & J.M. Lynch), pp. 30-43. Cambridge University Press.

Waterhouse, D., Dillon, B. & Vincent, D. (1998) *Economic benefits to Papua New Guinea and Australia from the biological control of banana skipper (Erionota thrax)*. ACIAR Impact Assessment Series IAS12. 36 pp. ACIAR, Canberra.

Zeddies, J., Schaab, R.P., Neuenschwander, P. & Herren, H.R. (2001) Economics of biological control of cassava mealybug in Africa. *Agricultural Economics* **24**, 209-219.

What is needed to improve the selection, testing and evaluation of weed biological control agents: Workshop synthesis and recommendations

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Summary

This biological control workshop, organised by the Co-operative Research Centre (CRC) for Australian Weed Management, included sessions on agent selection, host-specificity testing, and different aspects of evaluating weed biological control programs. A key purpose of this workshop was to enable scientists involved in weed biological control from northern and southern Australia to meet and discuss some of the critical issues of their discipline. This paper summarises the outcomes of the workshop discussions, which occurred following the presentation of a series of position papers, published in these proceedings, on each of the three afore mentioned aspects of biological control. Agent selection, while critical to project success, remains one of the least science-based activities in biological control. A number of techniques are now available to improve the science behind agent selection, including understanding the population dynamics and genetic structure of target and agent species and using molecular techniques and climate models for better target-agent matching. Recent scientific developments now allow for a complete reappraisal of the reasoning and process behind accepted host specificity testing procedure. A need was identified to develop new protocols for such testing, together with regulators, built around these modern scientific concepts. Impact evaluation, at a local and regional scale, can be helped by ecological models which can themselves provide the basis of economic models that predict or demonstrate the net benefits of weed biological control. Finally, this paper highlights key recommendations for future research that emerged from workshop discussions.

Key words: Host selection, host specificity, impact assessment, ecological modelling, economic modelling.

Introduction

In their introduction to this workshop, Briese *et al*. (these proceedings) pointed out that, despite substantial successes in the field of weed biological control, there were still critical issues concerning the science and practice of biological control that needed to be addressed. These issues have been brought about to a large extent by changes in the public perception and the increasing need to be accountable, both from an environmental and economic perspective. The ultimate purpose of the workshop was to identify where improvements could or should be made, and to provide the outline of a biological control research program for Australian researchers that would systematically and co-operatively address these issues.

Following the presentation of the respective position papers published in these proceedings, workshop discussions were held in smaller groups followed by a plenary session for each of the three topics of interest; agent selection, host specificity testing, and the evaluation of biological control success.

This paper attempts to capture the debate and conclusions of these workshop sessions. As such we do not attempt to provide all the answers to issues raised. At the specific level, it is intended to provide guidance for the research to be undertaken during the life of the Cooperative Research Centre for Australian Weed Management. However, the issues have a general applicability to weed biocontrol as a practice worldwide and, allowing for regional differences in economic and political landscapes, their resolution will improve the efficiency and overall success of the discipline.

Biological control attempts have often failed. Increasing our ecological understanding of potential biological control systems may allow us to better predict those systems in which biological control may be successful, and avoid implementing biological control on those systems that will likely fail. Continued monitoring and evaluation of current biological control programs may aid our understanding. The participants of the workshop therefore hope that these outcomes may also help to stimulate research on the core issues of weed biological control on a broader scale.

First some definitions; a target weed is a weed species that is the focus of a control program, while a biological control agent is the species released on to the weed in an attempt to control it.

Agent selection

The success rates of biological control agents have not greatly improved over the past 40 years. Further development of the following topics was identified as having the potential to improve the efficiency of choosing effective biological control agents from amongst the pool of candidate species for each target weed:

- Weed population dynamics and effective control agent communities
- Agent genetic diversity
- Climate modelling
- Limiting factors to research in the native range
- Selecting agents with low risk of predation
- Use of genetically modified (GM) agents

Weed population dynamics and effective control agent communities

One approach to improving agent selection is to study the target weed to define the type of damage required to ensure effective population suppression (McEvoy & Coombs, 1999; Sheppard, these proceedings). This in turn may lead to the selection of an effective control agent community to achieve these types of impact. Such studies may provide answers to key questions such as which part of the plant should we target agents against (i.e. which insect guild to select) and which stage of the weed lifecycle is most vulnerable to damage. Where multiple agents are likely to be introduced a process of prioritisation is required to enhance agent complementarity, avoid competition and maintain pressure on the target weed. It is also likely to be too costly to do these detailed ecological studies for each weed target. Therefore, generic solutions require development, for example across weeds of similar life history.

Successful agent establishment and acceptable rates of spread are also important in choosing effective agents. One recommendation for understanding which factors are important in agent establishment and spread was to adapt weed decision support such as Weed Risk Assessment (Groves *et al.*, 2001) to biocontrol agents. This might improve selection of successful agents, as predicting agent establishment and spread has direct parallels to disciplines involved in predicting invasions of non-indigenous pests (CSBPIPNPPPUS, 2002). However, there are parallel concerns with such approaches (Sheppard, these proceedings). Guidance in predicting agent establishment and spread is also likely to be available in the insect biological control literature.

Agent genetic diversity

Modern molecular methods are making it far easier to characterise the genetic diversity and subspecific phylogenetic structure of agents prior to introduction. These approaches are equally important for describing the target weed populations. A desire to know and characterise exactly what agent material is to be released will lead to a more widespread application of these techniques, particularly where there is clear evidence of subspecific variation within agent species.

As a result, we will be able to initially manage the diversity of a biocontrol agent through either capturing maximum diversity or restricting diversity to more specific or matched subspecific entities. Where a species of potential agent is fairly homogeneous at least with respect to specificity, maintaining maximum diversity is perhaps desirable to ensure a capacity for establishment and spread throughout the whole exotic range of the target weed, and is most easily achieved by collecting from as many agent populations as possible. The greatest diversity is expected from the evolutionary origin of the host.

Where apparent subspecific divisions occur (e.g. subspecies, strains, biotypes and clear phylogenetic clades) a strategy of regulated diversity might be preferential, e.g. importing a limited sample such as one population. This will ensure that, where there is likelihood that wider genetic diversity may involve more variable host specificity, only the agent populations tested for specificity are introduced. Host specificity and host compatibility of different biotypes of a potential agent will therefore require separate risk assessment before release. Anomalies do occur in host testing where there is genetic variation in the mechanisms defining host specificity of biological control agents. Resolution of such anomalies may require the determination of host specificity and compatibility of each population.

Climate modelling

The prediction of agent abundance following release is important, but difficult, as it results from interactions between the agent and its new biotic and climatic environment. Developing climatic modelling alongside our understanding of agent ecology may assist in predicting agent abundance, or will at least allow better climatic matching between an agent's native range and where it is required to provide effective control. Developing our understanding of the environmental factors important for agent development and population increase will be important. This may be most straightforward in wet tropical systems where agents more frequently undergo continuous generations and have fewer dormancy requirements and strategies. There are examples where agents are effective in some climates and not in others (van Klinken *et al.*, 2002). Retrospective studies of well known agent weed systems that have shown different degrees of success may provide a useful tool for assessing the value of more detailed climatic matching.

Limiting factors to research in the native range

Two main practical factors were identified that limit a capacity to conduct the detailed native range studies of agents and targets needed to make agent selection decisions; firstly, funding levels, and secondly, political and infrastructural restrictions to personal safety and lack of laboratory facilities. Funding levels also restrict ecological work in the country of introduction, which is counterproductive for funding agencies, as it prevents effective future evaluation of their investment.

Selecting agents with low risk of predation

Generally, exotic organisms suffer less parasitism in the introduced range than in their native range, providing a greater potential for high population density when used as biological control agents. However there are arguments both for and against using agents that are highly parasitised in their native range. Target weeds that show high abundance in both their native and exotic ranges can only be successful controlled by agents escaping native parasitism following release in the exotic range suggesting high native parasitism rates suggest a good agent. However, there is a positive correlation between the numbers of parasitoids attacking hosts in the native range and the number of parasitoids attracted following introduction in the exotic range (Cornell & Hawkins, 1993). This might suggest against selecting species heavily parasitised in their native range as biocontrol agents. Numerous studies have shown that insect biocontrol agents exposed to generalist predation suffer from lower establishment success in Australia. Long recognised recommendations for selecting agents that have predation/parasitism limited population dynamics, protected feeding niches or effective predation defence mechanisms (Harris, 1991) still seem to be valid.

Use of genetically modified (GM) agents

Genetic modification is being considered in a number of biological control programs against vertebrate pests. Therefore, its value and use in weed biological control should not be ignored. The use of genetically modified pathogens to increase virulence or carry genes that sterilise the target (a tactic under investigation for rabbit control in Australia) may provide future generations with profitable avenues of research.

Host specificity

Given the recent reviews of the methodology of testing procedures (van Driesche *et al.*, 2000; Withers *et al.*, 1999), this workshop focused on procedures for selecting plants to be tested, and a consideration of work required post-release to verify the outcomes of host-specificity testing. Six areas of research were distilled from the group discussions of where host-specificity testing could be improved:

- Application of molecular phylogeny to compiling host test lists
- Statistical rigour and framing null hypotheses
- Quality of test plants
- Genetic variability and quality of agents
- Agent and target evolution
- Importance and predictability of non-target damage

Application of molecular phylogeny to compiling host test lists

Selection of test plant lists can greatly affect resulting interpretations of host-range of candidate biological control agents. There is general acceptance that, while the current methodology for selecting test-plant lists for host-specificity studies has served the biological control community well over the past 30 years, significant advances in several scientific disciplines and changed public perceptions of risk and accountability make it necessary to review current methodology.

Recent statistical approaches to host specificity test analysis (Briese & Walker, 2002) suggest that inclusion of some previously recommended criteria for test plant list selection provided no additional value for interpretation of agent host range, e.g. including any crop plant not previously exposed to the agent, or host plants of insects closely related to the agent (Wapshere, 1974). The main purpose of further refinement of test plant list selection would be to take advantage of the growing body of information on plant phylogenetic relationships and of recent studies of the evolution, physiology and behaviour of host-choice in specialised organisms. A critical initial task in this process would be to review the scattered literature on these topics from a biological control perspective.

A more phylogenetic approach to test list selection incorporating ecological and biogeographical similarity between test plants and target weeds (Briese, these proceedings) may focus testing on better defining host range and more accurately assessing the risk of releasing an agent into a new environment.

This approach may be validated by reviewing past host specificity studies and exploring anomalies (i.e. where potential agents have been found attacking distantly related species). Also, a review of the role of secondary plant chemistry and plant morphology in agent host selection may be fruitful.

Changes to accepted practice in test list selection should be developed with the full participation and acceptance of regulatory authorities, such as Environment Australia and Agriculture, Fisheries and Forestry - Australia (Australian Quarantine Inspection Service and Biosecurity Australia).

Statistical rigour and framing null hypotheses

Greater statistical rigour needs to be applied to host specificity testing. The null hypothesis should be framed to clearly address whether an agent is or is not monophagous. For example, “the agent will survive and reproduce on plant species A, B or C” defines host range, while “agent survival and reproduction will not vary for plant species A, B or C” more accurately defines host suitability and therefore host specificity (van Klinken, 2000). Quantitative data should therefore be collected during host specificity tests where possible, as this at the very least allows ranking and nonparametric statistical testing of the results (Briese & Walker, 2002). There is, nonetheless, scope for the use or development of more sophisticated statistical analyses for better quantification of host-specificity data.

Genetic variability and quality of agents

Host specificity testing requires a clearly defined test organism. For this, the origins and where possible the genetic variability of the test population need to be clearly defined. Guidelines for monitoring and maintaining genetic diversity in agent colonies used for testing may be appropriate. For example, culture lines consisting of the offspring of one or several closely related females might be a basis for laboratory colonies in analogy to single spore isolates used for testing of plant pathogens. If evidence exists of variability in host choice or suitability, several lines might be included in host specificity tests, followed by releases of hybrid lines. Recent work has also shown the importance of using lines that are not laboratory adapted or inbred (Clarke, 2001).

Agent and target evolution

The host specificity of an agent at the time of release can be estimated with acceptable accuracy. However, post-release evolutionary change in host range may still occur resulting in previously unacceptable or unsuitable plants becoming new hosts. A recent review of this area has concluded that this risk can be predicted by considering constraints, genetic variation and ecological context (van Klinken & Edwards, 2002). The time scale for evolutionary change needs to be considered. The speed at which change occurs will differ greatly among species. The construction of molecular phylogenies around the key agents proposed for introduction and mapping these on phylogenies of host plants attacked can also quantify risk of host switching based on its frequency of occurrence in the evolutionary history of the agent and its close relatives. Following release, it is also plausible that over a number of generations the agent and the host will evolve greater compatibility, exhibited as improved performance of agent on host plant. The application of these ideas would more clearly address the risks of post release change in host use by biocontrol organisms.

Importance and predictability of non-target damage

Predictions of risk to non-target organisms obtained through host specificity testing procedures need to be validated in the field following release. This would help address possible concerns that current risk assessment procedures are too conservative or risk averse. Acceptable levels of risk to non-targets may be higher than zero impact for some targets that pose severe threats to the environment or high levels of costs to agriculture.

Validating predictions about non-target effects following release of biological control agents can be addressed using a number of approaches: a) measuring per capita impacts of agents on non-targets under controlled conditions, b) recording occurrence and abundances of agents on non-targets in the field and c) population level or community level studies of non- or off-target effects of biological control agents

Suitable systems that already merit further studies of non-target impacts were identified by Willis *et al.* (these proceedings) as:

- Agents of fiddle dock (*Rumex pulcher*) in Western Australia
- Early agents released against Paterson's curse (*Echium plantagineum*) e.g. *Dialectica scalariella*
- The rust fungus, *Phragmidium violaceum*, released against *Rubus spp*. in Tasmania and New Zealand
- Agents of ragwort (*Senecio jacobaea*)
- *Neurostrota gunniella (*for *Mimosa pigra)* on *Neptunia major*
- Rubber vine moth *Euclasta whalleyi* (for *Cryptostegia grandiflora*) on *Gymnanthera* spp. away from rubber vine infestations.

Evaluation at a local scale

Agent establishment in space and time requires the assessment of agent population density as well as the level of damage to the target weed. At key sites evaluation programs can measure those variables most likely to reveal the population dynamics of the target and the other members of the vegetation community. Methodology for carrying this out, however, will frequently need to be developed on a case-by-case basis.

Impact on an individual plant

Preliminary glasshouse studies of how selected agents affect individual plants are useful. Such studies can provide measures of agent per-capita damage or biomass reduction and look at the relationship between agent load and reductions in survival or flowering of the target (Dhileepan *et al.*, 2000; Dhileepan & McFadyen, 2001; Morin *et al.*, 2002). Although glasshouse studies provide different measurements of impact compared to field studies, they can help sort out subtle agent effects on the allometry of resource allocation in plants to roots, shoots and reproductive structures that can then help calibrate damage observed in the field (Willis *et al.*, 1998). The data collected for individual plants can provide the basis for scaling up impacts to the population level, once the effects of plant size and density variation are understood (Sheppard *et al.*, 2001). Such studies can also provide relationships for the effects of agent density on individual agent performance. These data can provide a reliable source of information, which, together with population studies of the target weed at individual sites, can be used to construct ecological models of agent-target interactions (e.g. Sheppard *et al.*, 2002; Buckley *et al.,* 2003)

Field trials

Carrying out impact evaluation in the field, particularly through controlled experiments (e.g. Sheppard *et al.*, 2001), provides the most realistic impact data, particularly for estimates of seed production, seed viability, root growth/biomass (which is important for plant survival), weed population size/age structure and seedbank sizes. Pesticide exclusion trials are also most effectively done at the local scale (Dhileepan, 2001).

Deciding which parameters will be the most important to measure will depend on weed life history traits and so will need to be defined on a case-by-case basis. Field trials can also allow studies of indirect impacts mediated through competing desirable plant species, as it will be important to have data to support claims that short term declines in weed abundance lead to short-term increases in desirable species (Sheppard, 1996).

Regional evaluation

Evaluation programs should ideally measure those variables most likely to reveal the population dynamics of the target and the other members of the vegetation community. However, the resources required to achieve this at a regional scale are always prohibitive. Regional scale evaluation of biological control projects, therefore, aims to build on local scale evaluation, by using easily collectible data that can assist in scaling up and estimating population level impacts over regions.

Effective planning

Evaluation on a regional scale is costly and therefore requires full funding agency and stakeholder support before instigation. Funding for such evaluation usually only becomes available once there are indications that there is an impact worth evaluating. Setting up an evaluation procedure may, therefore, be pointless if the agent impact is not obvious (e.g. because agent population density remains low). Once agent impact is obvious, however, regional evaluation becomes critically important, particularly for biological control agents with slowly spreading impacts and, consequently, longer time frames in reducing weed abundance. The notoriously subjective categories of "partial" or "substantial" control in analyses of biological control success can only be objectively quantified using regional level evaluation. Most biological control projects do not achieve full weed control so poor quantification of such cases will undervalue the discipline. Regional evaluation needs to be linked in turn to an economic evaluation.

Outlining an evaluation strategy up front, i.e. stating clearly what the goals and deliverables will be with reference to the quality and quantity of data required to achieve them, is a key to success (Swirepik & Smyth, these proceedings). Most evaluations of biological control fail due to lack of planning, particularly concerning the availability of funds. The choice of sites for long-term evaluation is also crucial, because of funding constraints, and yet those sites that are selected will need to represent variation in habitat and climate within the target weed's distribution.

Which parameters to measure and data to collect?

Regional scale evaluation must be largely based on before-and-after data or, preferably, changes over time at many sites. Data collection has to be limited, due to the scale of the assessment and the lower skills base of many of the extension staff involved.

Evaluation focuses around carefully selected parameters, which will depend on the original declared aims of the evaluation process. Where evaluation aims to detect a decline in target density, for example, then counting plants or measuring the size of seedbanks over time may be sufficient (Sheppard *et al.*, 1999; Swirepik & Smith, 2002). However, if evaluation also aims to measure indirect benefits to desirable species, then biomass change in the target or even some beneficial indicator species over time might be a more appropriate parameter.

The precise data collected also requires careful thought to minimise effort without compromising the impact estimates. For example, in evaluating Paterson's curse biological control, local scale evaluation appeared to show that a reasonable estimate of seed loss per unit area could be obtained from field estimates of only two parameters; mean plant size and the percentage of plants attacked by an agent (Sheppard *et al.*, 2001).

How long should evaluation continue?

How long evaluation projects might run is related to how long agents will need to be redistributed, and is therefore likely to be, at least partly, agent specific. Regional evaluation should continue for at least as long as agent redistribution, since the activities can be complementary and coordinated. Such evaluation may help decide where agent redistribution should be promoted and when it is no longer necessary. Ideally evaluation of biological control projects should run until their full effects can be measured, but the resources required to achieve this are invariably prohibitive.

Scales of evaluation?

Regional impact assessment carried out in some temperate pasture weed projects has used three levels of impact assessment, from detailed impact assessment at release sites by the research team, through basic monitoring over a greater number of sites to low level monitoring of key data types (e.g. agent presence, distance spread etc.) by skilled teams (Swirepik & Smyth, these proceedings). Discussion on the adequacy of different levels of evaluation for impact assessment at a regional scale led to the view that it would be difficult to manage several levels of impact monitoring across diverse networks of agency staff and stakeholders. However, there might be cases where two levels would be sufficient if, for example, some local-scale evaluation had already been completed or if damage was too obvious to necessitate detailed evaluation.

Useful recent techniques

The use of remote sensing and the increasing sophistication of modern mapping packages could also be a valuable aid to regional scale evaluation, although the lack of compatible pest mapping systems between organisations may require a fresh approach for widespread weeds. In biocontrol programs, where either the target or the agent or both are made up of hard to separate multi-species systems, molecular markers can help track the different strains of agent or help in quantifying impacts across the different target taxa.

Regional evaluation is the first step to economic evaluation and so focuses on relationships between agent versus weed density and weed biomass reductions and large scale agent spread.

Role of models in evaluation

Why model?

Ecological models in weed biological control generally serve two roles; explaining what is observed and predicting what might happen in the future (Barlow, 1999). Understanding the ecological population processes in agent-weed interactions naturally leads to using the developed understanding (the model) to make predictions for a range of questions relating to agent effectiveness. Models also allow exploration of the population dynamics of the agent-weed system as the agent, or at least its impact, can be easily added or removed from the model (Lonsdale *et al.*, 1995).

An effective use of a modelling approach from the start of a biological control program is to clearly define the questions to be addressed and use these questions to develop at least a conceptual model of the relevant processes and interactions. Most ecological models are just mathematical extensions of conceptual models (Shea, 1996). Modelling imposes structured thinking on the project, where different models can be trialled and dropped as appropriate. Access to modelling expertise is comparable to access to a statistician in the planning stage of experimentation. If the plan includes a model from the start, then the data collection can be strategically defined for the model to answer the necessary questions. This prevents projects wasting valuable resources collecting data that is surplus to requirements for efficient biocontrol evaluation.

Working together from the start, a modeller and biocontrol practitioner may be able to understand, a) the types of agent likely to be most effective, b) the ecological interactions between the selected agent and the target and, c) the likely secondary and subtle effects of establishing a biocontrol agent on the target. The subsequent use of models in the evaluation phase then simply becomes an extension of model usage from the "ecological understanding" phase of the project (Hoffmann, 1990). An existing model describing the key agent and weed parameters will quickly help to define the important parameters to measure during the evaluation phase. Where models can provide a clear understanding of the state of play in a biological control program from the start, they may help maintain funding support for projects where impacts are slow to appear.

Modelling, like statistical expertise, is a skill frequently left out of biological control projects when funding is limited. To justify the expense of including modelling in a biocontrol project, it is necessary, but often difficult, to demonstrate how models can accelerate the benefits of the project. Modelling is more frequently employed later in projects once some significant success (Smith *et al*., 1984; Akbay *et al.*, 1991; Lonsdale, 1996) or failure (Powell, 1990; Kriticos *et al*., 1999) has renewed interest from the funding agencies. Too much may be expected of modelling, however, when it is only involved in the latter stages of the project. The increasing availability of generic and highly adaptable population modelling platforms such as DYMEX® (Maywald *et al.*, 2003), which allow scientists to develop their own models of biological control systems with little direct need for programming skills, may help their more systematic usage.

Prediction versus evaluation

Increasingly weed population-based models are being used to make predictions, both in agent selection (Smith *et al*., 1993) and post-release evaluation (Sheppard *et al.,* 2002). These activities are closely related, because a capacity to predict which types of agent damage are most likely to reduce weed abundance allows prediction of long term impacts from agents that are still spreading and increasing in density. Ecological models can also suggest benchmark damage levels required before an impact of an agent on weed population density can be measured.

The desire to use the predictive capability of such models requires extreme caution and a conservative approach, as such predictions may be grossly inaccurate. The accuracy and reliability of such predictions always requires validation. Where models can provide reliable predictions, this may help save resources by reducing the necessity for repeated detailed field evaluation.

In a similar way, models can be used retrospectively to understand why particular agents worked (Lonsdale *et al.*, 1995) or failed (Powell, 1990). This has general relevance to improving success rates in biocontrol. Modelling also provides assistance when particular biological control projects appear to have achieved only partial success (Akbay *et al.*, 1991). In this capacity, such models may also be able to suggest what other management strategies or agent types may complement the biological control agent (Kriticos *et al*., 1999; Rees & Hill, 2001).

Model complexity

There is an increasing range of model types and modelling approaches available, and their suitability and level of complexity required will vary with the question(s) being asked. Simple models allow development of a generic modelling approach applicable to, for example, a range of weeds in a particular functional group (e.g. Rees & Hill, 2001). Simple models will still provide benchmark levels of damage required to impact an average weed population but cannot deal with the details of, for example, the complex impacts of environmental variation on agent impact.

In Australian weed systems, climate is often a limiting factor in agent impact. Having models that accurately reflect this requires climate driven models, where climate drives the growth and phenology of the weed and agent populations (Stuart *et al.*, 2002). Such simulation models can incorporate increasing levels of complexity as more and more is known about the ecophysiology of weed-agent system. Climate models may be useful to understand, for example, where agents will be well synchronised with their hosts, and why agent effectiveness varies across different climates

(Kriticos, 2001). This allows extrapolation from evaluation at the local to the regional scale. Such models could also suggest the optimal location of release sites to assist agent redistribution or indicate where other weed management approaches will be required.

Economic evaluation

Benefit-cost analyses

Economic analysis in biological control projects traditionally takes the form of benefit-cost analyses during project definition. Because of the long-term ecological nature of the changes biological control can bring about and the relatively small associated costs, such analyses rarely drop below a benefit-cost ratio of 10:1, even when significant risks of failure are acknowledged. This often appears to vary little irrespective of the number of unknowns or the accuracy of data to support predictions. The economic data on which such analyses are based for weeds outside intensive agricultural systems is usually largely speculative and yet such weeds pose the biggest threats to the Australian environment. The need for better ways to assess natural heritage values of the Australian environment rather than purely by lost production costs of such weeds is important for future investment in weed biological control.

Funding agencies will increasingly need to accurately evaluate potential benefits of biological control. This is hardest to achieve for rangeland weeds and weeds invading natural habitats. The spatial problems or threats that such weeds pose are often enormous. Their importance is currently only measured by the area they infest in relation to the strategic importance of the areas in which they occur. The extensive scale and inaccessibility of rangeland weeds and often low land values compromises sensible estimation of the likely economic returns from biological control projects. Despite this, biological control frequently offers the only long-term management option. Economic evaluation needs to develop better ways of calculating land amenity values in addition to changes in agricultural returns, but how best to do these remains unclear.

Economic evaluation

Economic evaluation of biological control projects once significant weed reduction has started to be observed is still in its infancy. Analysis of the investment made by the CRC for Weed Management Systems in this area demonstrated high potential returns on investment (CRC, 2001). Such analyses may include using local scale impacts to predict what final benefits might be over the whole range of the weed (e.g. Nordblom *et al.*, 2002; Nordblom, these proceedings) or retrospective analyses of projects where the greater part of the success has been observed. Such analyses differ only in that waiting for success to have happened allows assessment of actual over potential benefit. For most projects where success arrives slowly, such evaluation is the best way of maintaining stakeholder investment in the project. For example, considerable past investment in biological control of rangeland weeds is now leading funding agencies to question what the returns are for their investment.

Ecological models are best placed to provide the structure and ecological data needed for bioeconomic analyses of projects showing success. Without using bioeconomics to demonstrate the value of long-term investment in a natural resource management tool like biological control, future stakeholders will continue to invest in shorter-term solutions because of perceived lower risk of failure and faster likely benefits. It also seems likely that only clear evaluation of successful projects will lead to increased overall investment in biological control. As systematic a use as possible of such economic evaluations for biological control projects nearing fruition should be given high priority.

The development and design of generic economic models that might need only a few parameters (i.e. cost of weed ha^{-1}, benefits of biological control ha^{-1}, area affected) would prevent the need for a bioeconomist and economics model for each weed project.

Economics of agent redistribution

Economic evaluation is also assisting the design and duration of biological control agent redistribution programs, for projects where success dependent on agent dispersal rates. Significant benefits have been identified from investment in coordinating agent redistribution networks across southern Australia (CRC, 2001) and a recent study allows predictions to be made on the potential region by region economic returns from further agent releases (Nordblom *et al.*, 2002). Agent redistribution for rangeland weeds may benefit from such an approach. Such activities are costly, raising questions about the economic value of large numbers of local releases to individual properties verses fewer releases at a larger scale e.g., local government areas. To carry out such analyses, however, the rate of agent spread, attack rates over time, the impact of different attack rates, and the environmental limitations on spread and effectiveness need to be known.

Summary recommendations

This section summarises some general recommendations from the workshop relevant for future biological control activities in Australia.

Agent selection

Studying the dynamics of problem weed populations to define where to target damage and how much damage is required to suppress weed abundance, is critical for effective selection of any approach to weed management. This is the first priority of any weed biological control project.

Simple molecular tools now available allow clear target and agent definition within an evolutionary context. It would only seem responsible to use such tools each time a potential biological control agent is being considered, especially if there is any hint of within species variation in host specificity. Selection can then be made of the agents likely to be most effective. Procedural protocols still need to be put in place to allow risk assessment to continue effectively without the need to screen each genetic entity against a whole host plant test list.

Climate matching is still a valid rule of thumb for agent selection, especially where agent abundance is also a known variable. Incorporating such information into agent based climate models may enhance this process.

Where native range studies are inappropriate, closer scrutiny of the insect biological control literature may provide ways of predicting agent establishment and spread. Selecting agents that can escape predation in the introduced range should remain a key criterion for introduction.

Using genetically modified biological control agents is being trialled in vertebrate pest control programs. Its future use for weed biological control should not be discounted.

Host specificity

Practitioners involved in generating host plant test lists should take advantage of the growing literature of plant phylogenies and of the evolution, physiology and behaviour of host-choice in specialised organisms. A critical initial task in this process would be to review the scattered literature on these topics from a biological control perspective. Host specificity tests should, in future, address clearly defined hypotheses to remove confusion about the purpose of such tests. These should generate quantitative data on host use for the less monophagous agents so that the true value of including some traditionally tested plant groups can be clearly evaluated. It might soon be possible to revise host testing procedure and agent risk assessment in general, in collaboration with the regulatory authorities, into a more tightly justified and modern process to take full advantage of recent scientific developments.

Guidelines for monitoring and maintaining genetic diversity in agent colonies used for testing may be appropriate to ensure we know what is released and to prevent colony inbreeding problems.

Molecular tools now allow estimation of the risk of host switching following release. This is linked to the importance of co-evolutionary processes in agent evolution. Work should be more widely recognised and encouraged in this area. Also, evidence is needed to determine whether or not agents improve their performance on targets in the generations after release.

Host specificity testing is a process of predicting non-target usage or impact. But such predictions are rarely tested. Where non-target effects seem likely these could be systematically tested in the field after release. This would improve our understanding of the value of agent testing to demonstrate likely off-target effects. Suitable systems where such testing might already start have been listed.

Evaluation at a local scale

One priority might be to improve agent impact assessment methodology. This might be achieved through a comparative approach by using a number of different cases within each plant life history functional group (e.g. annual herbs, woody legumes, vines). Methodology is also likely to vary with the feeding guild or mode of action of the agents(s), and the type of damage observed. Example systems for such work might include rubber vine, cat's claw creeper, bellyache bush, *Parthenium*, bridal creeper and Paterson's curse.

Regional evaluation

A key requirement is the definition of core parameters requiring estimation when evaluating weed targets in different functional groups. Parameter requirements may differ where assessing direct impacts alone or where impacts are linked to direct or indirect assessment of benefits to non-targets. The costs of regional evaluation will be directly related to the time required to collect and process these data. It will be important, therefore, to select the best data to produce quick and reliable estimates of these parameters.

Models for evaluation

Many practitioners doubt the value of a modelling approach in weed biological control evaluation, despite an increasing number of published examples. Consolidating the role of modelling in this area might benefit from extending published reviews in this area (e.g. Barlow, 1999) or by reviewing the value of models in case studies. Understanding the relevance and benefits of differing modelling approaches and the role of simple versus complex models needs further work. Practitioners will increasingly require generic models or modelling platforms for a range of tasks, e.g. optimising the redistribution of agents or evaluating agents for weeds of particular functional groups.

Economic evaluation

Efforts to improve predictions on the value of biological control through improved cost-benefit analyses might focus on new target weeds, such as bellyache bush (weed spread and economic losses assessed in relation to the spread of agent impact) or sowthistle control in the northern cropping zone (analysis of the advantages versus costs of attempting biological control through a reduction in herbicide use). Past successful projects and those nearing fruition, where economic evaluation may be used include; prickly pear, St John's wort, skeleton weed, ragwort, *Onopordum* thistles, rubber vine, *Salvinia*, *Sida*, parthenium and *Mimosa pigra*. Finally, such economic assessments could usefully incorporate other management options to determine the value of integrating control techniques, e.g. Rees & Hill (2001) predict biocontrol of gorse will enhance other control strategies, providing a basis for assessing benefits of gorse biocontrol agents released 70 years ago.

Conclusion

The authors hope that this synthesis paper encourages greater use of the scientific approach to the development of biological control host selection, host specificity and impact evaluation. Biological control is going through some testing times with perceived low success rates compounded by increased perceived environmental risks in its practice. These present new challenges for the discipline that need to be surmounted for biological control to remain a viable tool in the battle against weeds.

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References

Akbay, K.S., Howell, F.G. & Wooten, J.W. (1991) A computer simulation model of water hyacinth and weevil interactions. *Journal of Aquatic Plant Management* **29**, 15-20.

Barlow, N,D. (1999) Models in biological control: a field guide. *Theoretical approaches to biological control* (eds B.A. Hawkins & H.B. Cornell), pp 43-68, Cambridge University Press.

Briese, D.T. & Walker, A. (2002) A new perspective on the selection of test plants for evaluating the host-specificity of weed biological control agents: The case of *Deuterocampta quadrijuga*, a potential insect control agent of *Heliotropium amplexicaule. Biological Control* **25**, 273-287.

Buckley, Y.M., Rees, M., Sheppard, A.W. & Smyth, M. (2003) Impact of biocontrol on the invasive plant *Echium plantagineum*: a coupled plant-herbivore model. *Ecological Applications*, in press.

Clarke, C. (2001) Climate matching in the colonisation of biological control agents against *Chrysanthemoides monilifera* and *Marrubium vulgare*. Ph.D. Thesis, Adelaide University.

CRC for Weed Management Systems (2001) *The CRC for Weed Management Systems: An impact assessment*, CRC Technical Series No. 6, Adelaide, Australia http://www.weeds.crc.org.au/documents/tech_series_6.pdf

Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States (2002) *Predicting Invasions of Nonindigenous Plants and Plant Pests*. Board on Agriculture and Natural Resources, Washington.

Cornell, H.V. & Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *The American Naturalist* **141**, 847-865.

Dhileepan, K. (2001) Effectiveness of introduced biocontrol insects on the weed *Parthenium hysterophorus* (Asteraceae) in Australia. *Bulletin of Entomological Research* **91**, 167-176.

Dhileepan, K. & McFadyen, R.E. (2001) Effects of gall damage by the introduced biocontrol agent *Epiblema strenuana* (Lepidoptera: Tortricidae) on the weed *Parthenium hysterophorus* (Asteraceae). *Journal of Applied Entomology* **125**, 1-8.

Dhileepan, K., Setter S. & McFadyen, R.E. (2000) Response of the weed *Parthenium hysterophorus* (Asteraceae) to defoliation by the introduced biocontrol agent *Zygogramma bicolorata* (Coleoptera: Chrysomelidae). *Biological Control* **19**, 9-16.

Groves, R.H. Panetta F.D. & Virtue J.G. (2001) *Weed risk assessment.* CSIRO Publishing, Collingwood.

Harris, P. (1991) Classical biocontrol of weeds: Its definition, selection of effective agents, and administrative – political problems. *Canadian Entomologist* **123**, 827-849.

Hoffmann, J.H. (1990) Interactions between three weevil species in the biocontrol of *Sesbania punicea* (Fabaceae): the role of simulation models in evaluation. *Agriculture, Ecosystem and Environment* **32**, 77-87.

Kriticos, D.J. (2001) Use of Simulation Models to Explore the Effects of Climate Change on Woody Weeds in Australia. Ph.D. Thesis. University of Queensland

Kriticos, D.J., Brown, J.R., Radford, I.D. & Nicholas, M. (1999) Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control* **16,** 230-9.

Lonsdale, W.M. (1996) The balance of weed populations. *Frontiers of population ecology* (eds R.B. Floyd, A.W. Sheppard & P.J. De Barro), pp. 573-589, CSIRO Publications, Melbourne.

Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995) Biological control of a tropical weed: a population model and experiment for *Sida acuta. Journal of Applied Ecology* **32**, 391-399.

Maywald, G.F., Sutherst, R.W. & Zalucki, M. (2003) *Dymex: Modelling natural ecosystems.* http://www.ento.csiro.au/dymex/dymexfr.htm

McEvoy, P.B. & Coombs E.M., 1999. Biological control of plant invaders: Regional patterns, field experiments, and structured population models. *Ecological Applications* **9**, 387-401

Morin, L., Willis A.J., Armstrong, J. & Kriticos, D. (2002) Spread, epidemic development and impact of the bridal creeper rust in Australia: summary of results. *Proceedings of the13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 385-388. Plant Protection Society of Western Australia, Perth.

Nordblom, T., Smyth, M., Swirepik, A., Sheppard A. & Briese, D. (2002) Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agricultural Economics* **27**, 403-424

Palmer, W.A. (1999) The use of cut foliage instead of whole plants for host specificity testing of weed biocontrol insects – is this an acceptable method? *Host specificity testing in Australasia: towards improved assays for biological control* (eds T.M. Withers, L. Barton-Browne & J. Stanley) pp 20-29. Scientific Publishing, Queensland Department of Natural Resources, Brisbane.

Powell, R.D. (1990) The functional forms of density-dependent birth and death rates of diffuse knapweed (*Centaurea diffusa*) explain why it has not been controlled by *Urophora affinis, U. quadrifasciata* and *Sphenoptera jugoslavica*. *Proceedings of the VIIth International Symposium on Biological Control of Weeds* (ed. E.S. Delfosse) pp. 195-202. MAF.Rome, Italy

Rees, M. & Hill, R.L. (2001) Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology* **38**, 364-377.

Shea, K. (1996) Estimating the impact of control efforts: models of population dynamics. *Plant Protection Quarterly* **11**, 263-265.

Sheppard, A.W. (1996) The interaction between natural enemies and interspecific plant competition in the control of pasture weeds. *Proceedings of the IXth International Symposium on Biological Control of Weeds*. (eds V.C. Moran & J.H. Hoffmann), pp. 47-54. University of Capetown, South Africa.

Sheppard, A.W., Smyth, M. & Swirepik, A. (1999) Impact of the root-crown weevil (*Mogulones larvatus*) and other biological control agents on Paterson’s curse in Australia: an update. *Proceedings of the 12th Australian Weeds Conference* (eds A.C. Bishop, M. Boersma & C.D. Barnes), pp 343-346. Tasmanian Weed Society Devonport, Tasmania.

Sheppard, A.W., Smyth, M. & Swirepik, A. (2001) The impact of *Mogulones larvatus* and pasture competition on *Echium plantgineum*. *Journal of Applied Ecology* **38**, 291-300

Sheppard, A.W., Rees, M., Smyth, M., Grigulis, K. & Buckley, Y. (2002) Modelling the population interactions between the crown weevil *Mogulones larvatus* and its host plant *Echium plantagineum*. *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 248-251. Plant Protection Society of Western Australia, Perth.

Smith, M.C., Holt, J. & Webb, M. (1993) A population model for the parasitic weed *Striga hermonthica* (Scrophulariaceae) to investigate the potential of Smicronyx umbrinus (Coleoptera: Curculionidae) for biological control in Mali. *Crop Protection* **12**, 470-476.

Smith, L.M.II, Ravlin, F.W., Kok, L.T. & Mays, W.T. (1984) Seasonal model of the interaction between *Rhinocyllus conicus* (Coleoptera: Curculionidae) and its weed host, *Carduus thoermeri* (Campanulatae: Asteraceae). *Environmental Entomology* **13**, 1417-1426.

Stuart, R.M., Kriticos, D.J. & Ash, J.E. (2002) Modelling the biological control of bitou bush (*Chrysanthemoides monilifera*: Asteraceae) by *Mesoclanis polana* (Tephritidae). *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 591-594. Plant Protection Society of Western Australia, Perth.

Swirepik, A. & Smyth, M. (2002) Biological control of broad-leafed pasture weeds (Paterson's curse, *Onopordum* and nodding thistles): What have we achieved and where to from here? *Proceedings of the 13th Australian Weeds Conference* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 373-376. Plant Protection Society of Western Australia, Perth.

van Driesche, R.G., Heard, T.A., McClay, A. & Reardon, R. (2000) *Host-specificity testing of exotic arthropod biological control agents: The biological basis for improvement in safety*. Morgantown, USA. USDA Forest Health Technology Enterprise Team, FHTET-99-1.

van Klinken, R.D. (2000) Host specificity testing: why do we do it and how can we do it better? *Proceedings: Host specificity of exotic arthropod biological control agents: the biological basis for improvement in safety* (eds. R. van Driesche, T. Heard, A. McClay & R. Reardon), pp. 54-68, Forest Service, Morgantown, West Virginia.

van Klinken, R.D. & Edwards, O.R. (2002) Is host specificity of weed biological control agents likely to evolve rapidly following establishment? *Ecology Letters* **5**, 590-595.

van Klinken, R.D. Fichera, G. & Cordo, H. (2002) Targeting biological control across diverse landscapes: the release, establishment, and early success of two insects on mesquite (*Prosopis* spp.) in Australian rangelands. *Biological Control* **26**, 8-20.

Wapshere, A.J. (1974) A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology* **77**, 201-211.

Willis, A.J., Ash, J.E. & Groves, R.H. (1998) Interactions between plant competition and herbivory on the growth of *Hypericum* species: a comparison of glasshouse and field results. *Australian Journal of Botany* **46**, 707-721.

Withers, T.M., Barton Browne, L. & Stanley, J. (1999) *Host specificity testing in Australasia: Towards improved assays for biological control*. Scientific Publishing, Queensland Department of Natural Resources, Brisbane.

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