BIOCONTROL OF WEEDS: ACHIEVEMENTS TO DATE AND FUTURE OUTLOOK

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ABSTRACT: New Zealand has a serious problem with unwanted exotic weeds. Invasive plants threaten all ecosystems and have undesirable impacts on primary production and biodiversity values, costing the country billions of dollars each year. Biocontrol is a key tool for reducing the impacts of serious, widespread exotic weeds. We review the nearly 90-year history of weed biocontrol research in New Zealand. Thirty-eight species of agents have been established against 17 targets. Establishment success rates are high, the safety record remains excellent, and support for biocontrol remains strong. Despite the long-term nature of this approach partial control of five targets (Mexican devil weed *Ageratina adenophora*, alligator weed *Alternanthera philoxeroides*, heather *Calluna vulgaris*, nodding thistle *Carduus nutans*, broom *Cytisus scoparius*), and good control of three targets (mist flower *Ageratina riparia*, St John's wort *Hypericum perforatum*, and ragwort *Jacobaea vulgaris*) have already been achieved. The self-introduced rust *Puccinia myrsiphylli* is also providing excellent control of bridal creeper *Asparagus asparagoides*. Information about the value of successful weed biocontrol programmes is starting to become available. Savings from the St John's wort project alone have more than paid for the total investment in weed biocontrol in New Zealand to date. Recent research advances are helping us to select the best weed targets and control agents, and are enabling biocontrol programmes to be even safer and more effective. Future challenges include expanding the range of targets to include more aquatic species, finding ways to do more for less given the number of weeds needing to be controlled, and developing bioherbicides through to commercially available products. The implications of climate change need to be kept in mind, but fortunately seem unlikely to substantially disrupt biocontrol programmes because biocontrol agents should be able to follow changes in weed distributions.

Key words: 90-year history, agent effectiveness, biopesticides, establishment success, excellent safety record, impacts on weeds, multi-targeting, prioritisation.

WEEDS IN NEW ZEALAND

New Zealand has a serious exotic weed problem. Early European colonists introduced more than 25 000 species of plants within a 200-year period (Williams and Cameron 2006), and newly introduced species soon naturalised and began causing problems. The first Act to control weeds in New Zealand was passed in 1854 (Thomson 1922), but weed problems have continued to worsen. Today the naturalised vascular flora of New Zealand (2430 species) exceeds the native flora (2414 species) (Paynter et al. 2010a). More than 20% of naturalised species are now recognised as weeds by a New Zealand government agency or primary industry (Williams and Timmins 2002) but they still occupy only a fraction of the suitable habitats, with much potential for further expansion (Figure 1). Weeds cost the country more than a billion dollars each year (Williams and Timmins 2002) and threaten all ecosystems. The potential pool of new weeds (plants still only in cultivation and not yet naturalised) is enormous (>30 000 taxa) (Williams and Cameron 2006). Biological control (biocontrol) is playing an important role in attempting to reduce the impacts of some of the most serious, widespread weeds.

FIGURE 1 Broom (*Cytisus scoparius*) covering hills in North Canterbury. Even widespread weeds like broom have not yet invaded all suitable habitat.

HISTORY OF BIOCONTROL

The early days

Research on biocontrol of weeds in New Zealand began at the Cawthron Institute, Nelson, in 1925 (Cameron et al. 1989). The earliest weeds targeted were agricultural pests: blackberry (*Rubus fruticosus* L. agg.), foxglove (*Digitalis purpurea* L.), gorse (*Ulex europaeus* L.), ragwort (*Jacobaea vulgaris* Gaertn.), and one native plant, piripiri (*Acaena anserinifolia* (J.R.Forst. & G Forst.) J.B.Armstr.). Between 1925 and 1931, 17 insects were imported for study but only the ragwort cinnabar moth (*Tyria jacobaeae* L.), gorse seed weevil (*Exapion ulicis* Forster), and piripiri sawfly (*Ucona acaenae* Smith) were released (Table 1) (Miller 1970). The latter failed to establish, but since piripiri and foxglove had begun to decline as the fertility of pastures was improved, no further efforts were made to develop biocontrol for these targets (Cameron et al. 1989). No agents were released against blackberry because all showed some potential to damage cultivated berries (Cameron et al. 1989).

Between 1931 and 1965 biocontrol faded into obscurity as new-generation herbicides became available and grew in popularity. The DSIR took over responsibility for the work, importing and releasing three agents for St John's wort (*Hypericum perforatum*

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TABLE 1 Weed biocontrol agents released in New Zealand

Agent	Target	Date first released	Estab-lished
Tyria jacobeae	*Jacobaea vulgaris*	1929	Yes
Apion ulicis	*Ulex europaeus*	1931	Yes
Antholcus varinervis (Ucona aecena)	*Acaena anserinifolia*	1936	No
Botanophila jacobaeae	*Jacobaea vulgaris*	1936	Yes
Botanophila seneciella	*Jacobaea vulgaris*	1936	No
Chrysolina hyperici	*Hypericum perforatum*	1943	Yes
Procecidochares utilis	*Ageratina adenophora*	1958	Yes
Zeuxidiplosis giardi	*Hypericum perforatum*	1961	Yes
Chrysolina quadrigemina	*Hypericum perforatum*	1963	Yes
Rhinocyllus conicus	*Carduus nutans*	1972	Yes
Urophora cardui	*Cirsium arvense*	1976	Yes
Ceutorhynchus litura	*Cirsium arvense*	1976	No
Altica carduorum	*Cirsium arvense*	1979	No
Agasicles hygrophila	*Alternanthera philoxeroides*	1981	Yes
Disonycha argentinensis	*Alternanthera philoxeroides*	1982	No
Lema cyanella	*Cirsium arvense*	1983	Yes
Longitarsus jacobaeae	*Jacobaea vulgaris*	1983	Yes
Arcola malloi	*Alternanthera philoxeroides*	1984	Yes
Trichosirocallus horridus	*Carduus nutans*	1984	Yes
Bruchidius villosus	*Cytisus scoparius*	1987	Yes
Tetranychus lintearius	*Ulex europaeus*	1989	Yes
Urophora solstitialis	*Carduus nutans*	1990	Yes
Agonopterix ulicetella	*Ulex europaeus*	1990	Yes
Sericothrips staphylinus	*Ulex europaeus*	1990	Yes
Cydia succedana	*Ulex europaeus*	1992	Yes
Arytainilla spartiophylla	*Cytisus scoparius*	1993	Yes
Scythris grandipennis	*Ulex europaeus*	1993	No
Phytomyza vitalbae	*Clematis vitalba*	1996	Yes
Phoma clematidina	*Clematis vitalba*	1996	Yes
Lochmaea suturalis	*Calluna vulgaris*	1996	Yes
Entyloma ageratinae	*Ageratina riparia*	1998	Yes
Monophadnus spinolae	*Clematis vitalba*	1998	No
Pempelia genistella	*Ulex europaeus*	1998	Yes
Urophora stylata	*Cirsium vulgare*	1999	Yes
Aulacidea subterminalis	*Pilosella* spp.	1999	Yes
Oxyptilus pilosellae	*Pilosella* spp.	1999	No
Procecidochares alani	*Ageratina riparia*	2000	Yes
Macrolabis pilosellae	*Pilosella* spp.	2000	Yes
Cheilosia urbana	*Pilosella* spp.	2002	Too early
Cochylis atricapitana	*Jacobaea vulgaris*	2005	Too early
Platyptilia isodactyla	*Jacobaea vulgaris*	2005	Yes
Cleopus japonicus	*Buddleja davidii*	2006	Yes
Cheilosia psilophthalma	*Pilosella* spp.	2006	Too early
Tortrix s.l. sp. *chrysanthemoides*	*Chrysanthemoides monilifera monilifera*	2007	Yes
Gonioctena olivacea	*Cytisus scoparius*	2007	Yes
Agonopterix assimilella	*Cytisus scoparius*	2008	Yes
Aceria genistae	*Cytisus scoparius*	2008	Yes
Cassida rugibinosa	*Cirsium* spp., *Carduus* spp.	2008	Yes
Ceratapion onopordi	*Cirsium* spp., *Carduus* spp.	2009	Too early
Gargaphia decoris	*Solanum mauritianum*	2010	Yes
Neolema ogloblini	*Tradescantia fluminensis*	2011	Yes
Lema basicostata	*Tradescantia fluminensis*	2012	Too early
Neolema abbreviata	*Tradescantia fluminensis*	2013	Too early

L.) and one for Mexican devil weed (*Ageratina adenophora* (Spreng.) R.M.King & H.Rob.) (Miller 1970; Cameron et al. 1989). All four agents established and neither of these weeds is a serious problem today – this can be attributed, at least in part, to these biocontrol agents.

The modern era

Growing disillusionment with herbicides led to a resurgence in biocontrol activity in the 1970s, and this activity has continued until the present. When the DSIR was disestablished in 1992, responsibility for weed biocontrol research shifted to the newly formed Landcare Research. Around this time, environmental weeds also began to receive more attention, and today the number of environmental weeds targeted for biocontrol exceeds agricultural weed targets.

Weeds targeted during the 1970s, 80s and 90s included gorse and ragwort (Figure 2), both for a second time, plus thistles (mainly nodding thistle *Carduus nutans* L., Californian thistle *Cirsium arvense* (L.) Scop., and Scotch thistle *Cirsium vulgare* (Savi) Ten.), broom (*Cytisus scoparius* (L. Link), hawkweeds (*Pilosella* spp.); the environmental weeds heather (*Calluna vulgaris* (L.) Hull), mist flower (*Ageratina riparia* (Regel) R.M.King & H.Rob.), and old man's beard (*Clematis vitalba* L.); and the only aquatic species tackled to date, alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb.). In total, 28 species of agents were released, including the first fungal pathogens (old man's beard fungus *Phoma clematidina* (Thüm.) Boerema, and the mist flower white smut *Entyloma ageratinae* R.W.Barreto & H.C.Evans).

The decade following the new millennium saw a strengthening of the attack on ragwort, thistles, and hawkweeds, with two more agents developed for each of these targets, and against broom, which was targeted with three more agents. A raft of new projects saw one agent released against boneseed (*Chrysanthemoides monilifera monilifera* (L.) Norl.), and another against buddleia (Buddleja davidii Franch.); the latter project was undertaken by Scion (formerly the Forest Research Institute). New projects targeting woolly nightshade (*Solanum mauritianum* Scop.) and tradescantia (*Tradescantia fluminensis* Vell.) have seen four species of agents released during the

FIGURE 2 Fields filled with ragwort (*Jacobaea vulgaris*) have become a rare sight since the establishment of the ragwort flea beetle (*Longitarsus jacobaeae*) (inset).

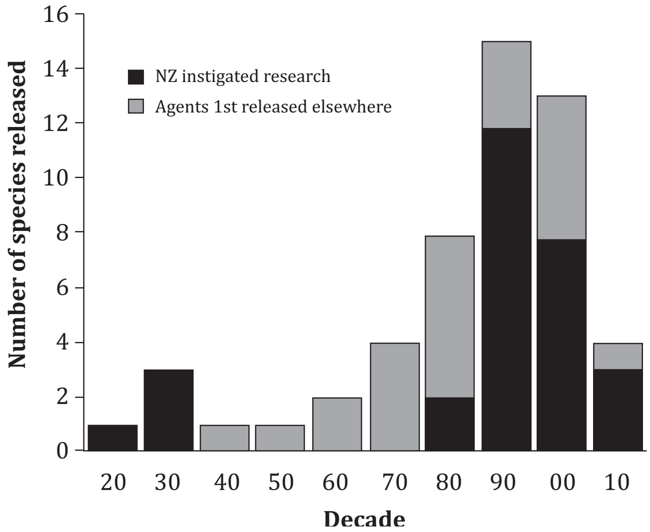

FIGURE 3 Weed biocontrol releases in New Zealand (counting only the first release per agent species).

current decade, with more planned.

One agent has recently been approved for release against moth plant (*Araujia hortorum* E.Fourn.) and another against Chilean needle grass (*Nassella neesiana* (Trin. & Rupr.) Barkworth), while two agents have been approved for each of Darwin's barberry (*Berberis darwinii* Hook.) and lantana (*Lantana camara* L.). Field releases of these new approvals are likely to begin in 2013/14.

Self-introductions

In addition to deliberately released weed biocontrol agents, many insects and plant diseases have established in New Zealand either accidentally or as self-introductions. At least four such species are helping to control weeds: broom twig miner (*Leucoptera spartifoliella* Hubner), hemlock moth (*Agonopterix alstromeriana* Clerk), blackberry rust (*Phragmidium violaceum* (Schultz) G.Winter), and most recently the bridal creeper rust (*Puccinia myrsiphylli* G.Winter). At least three of these species would have been considered for importation if they had not arrived naturally. In particular, no additional control of bridal creeper (*Asparagus asparagoides* (L.) Druce) has been required since the bridal creeper rust became well established.

Trends

The number of weed biocontrol agents released in New Zealand has substantially increased in the last 30 years (Figure 3) (Fowler et al. 2010). The earliest projects were against novel targets; these were followed by a period from the 1940s to the 1970s when New Zealand only acquired agents that had already been released elsewhere. More recently, projects have been a mixture of these two.

Thirty-nine (74%) of the 53 species of weed biocontrol agents released have targeted weeds that are problems mainly in the productive sector. However, since the 1990s the balance has tipped in favour of targeting environmental weeds, with 7 of the last 10 agents approved for release falling primarily into that category. Also, of the 12 targets for which agents are currently being sought (Table 2) only one, tutsan (*Hypericum androsaemum* L.), is primarily a productive sector weed, although pampas (*Cortaderia* spp.) and Darwin's barberry span both categories.

TABLE 2 Current targets for which new agents are being sought

Species	Location of native range surveys
Alligator weed *Alternanthera philoxeroides*	South America
Banana passionfruit *Passiflora* spp.	South America
Boneseed *Chrysanthemoides monilifera monilifera*	South Africa
Darwin's barberry *Berberis darwinii*	South America
Japanese honeysuckle *Lonicera japonica*	Japan
Moth plant *Araujia hortorum*	South America
Old man's beard *Clematis vitalba*	Europe
Pampas *Cortaderia* spp.	South America
Privet *Ligustrum* spp.	China
Tutsan *Hypericum androsaemum*	Europe
Wild ginger *Hedychium* spp.	India
Woolly nightshade *Solanum mauritianum*	South America

The source of agents has also changed for New Zealand instigated programmes: 18 of the 19 agents released before 2000 were of European origin compared with 7 of the 12 released since then. Current programmes focus strongly on weeds of South American origin, but surveys have also recently been undertaken in Asia and Africa.

ACHIEVEMENTS

Success gaining approval to release

New Zealand currently appears to be releasing biocontrol agents faster than any other country. Reasons for this include the seriousness of the weed problem; good continued public support for biocontrol; well organised end-user groups providing funding and support for projects (Hayes 2000); and excellent legislation that ensures decision-making is thorough, timely, and based on scientific evidence without political interference (Hill et al. in press). New Zealand has managed to avoid the serious opposition to biocontrol from lobby groups that has stifled progress in other countries (e.g. Stanley and Fowler 2003).

Robust decision making and consistent funding

The formation of the National Biocontrol Collective (regional councils nationwide and the Department of Conservation) has been a great asset. During the last decade this has allowed collective, nationally-focused decision-making about which weeds and agents to target, and has ensured consistent funding for projects. The development of projects and the mass-rearing and release of agents is mostly funded by this national biocontrol collective and the Ministry for Primary Industries, the latter via grants to interest groups from its Sustainable Farming Fund. Research to underpin the success and safety of weed biocontrol in New Zealand is funded by the New Zealand Government. Consistent funding and seamless integration between pure and operational research programmes have enabled all facets of weed biocontrol research to be tackled.

Successful establishment

By world standards our current success rate for establishing weed biocontrol agents is high (~85%) – this is nearly double the 44% success rate estimated for New Zealand 20 years ago (Cameron et al. 1993). Of the 53 species released in New Zealand to date, 3 involved one-off small token releases that, not surprisingly, did not establish and are not included in this calculation. Of the remaining 50 species, 38 have established and 6 have failed. The status of the other six is not yet known, so these are also excluded from the calculation. The high success rate is likely to be due at least in part to the network of biosecurity officers and land managers throughout the country who assist with finding suitable release sites, releasing agents, and subsequent monitoring. This network allows us to release more agents, more quickly and more widely than would otherwise be possible (Hayes 2000).

Research to optimise release strategies has also improved the success rate. Releasing agents at a large number of sites has been shown to be beneficial because it reduces the risk of known barriers to establishment, such as the detrimental effect of rain on newly released populations (Hill et al. 1993; Norris et al. 2002). The trade-off is that each release must comprise fewer individuals because the number that can be produced at any one time by mass-rearing is limited. While extinction risk increases with small releases (Memmott et al. 2005), relatively small numbers, e.g. <100 individuals per release for gorse thrips (*Sericothrips staphylinus* Haliday), can still have a high success rate (80%); consequently, 10 releases of this size is a better strategy than a single release of 1000 thrips that may still fail (Memmott et al. 1998). Where possible, information on optimal release size is obtained early in a programme so it can help subsequent redistribution strategies.

Successful programmes

Funding and logistical constraints mean many successful programmes have been assessed to only a limited extent (Table 3); examples of these limited assessments include quantitative studies of St John's wort and alligator weed, largely observational reports on Mexican devil weed (all reviewed in Cameron et al. 1989), surveys and experimental studies of ragwort (Gourlay et al. 2008), and modelling for nodding thistle (Shea and Kelly 2004). An exception is the mist flower biocontrol programme

FIGURE 4 Mist flower (*Ageratina riparia*) before (left) and after (right) the release of the white smut fungus (*Entyloma ageratinae*). Inset: the impacts of the white smut and gall fly (*Procecidochares alani*) have been shown to be additive.

where detailed studies showed that the white smut fungus caused major damage to the weed and mean percentage mist flower cover had declined after 5 years from 81% to 1.5% (Figure 4). This decline was accompanied by increased species richness and percentage cover of native plants, with only a weak 'replacement weed' effect (Barton et al. 2007). Detailed studies of the heather biocontrol programme have also shown a large (99%) reduction in heather cover from an isolated beetle outbreak and signs of native species recovery. This study also demonstrated how biocontrol can be at least as effective as herbicide while also avoiding non-target impacts (Peterson et al. 2011 unpubl. report; Landcare Research unpubl. data).

TABLE 3 Successful projects to date

Target	Level of success	Extent of monitoring
Alligator weed *Alternanthera philoxeroides*	Partial; good control in static water bodies	Good
Broom *Cytisus scoparius*	Partial, less vigorous in some areas	Ongoing (excellent)
Heather *Calluna vulgaris*	Partial, good control in areas with beetle outbreaks	Ongoing (excellent)
Mexican devil weed *Ageratina adenophora*	Partial, still common but less of a threat now	Almost none
Mist flower *Ageratina riparia*	Complete, no other control required	Excellent
Nodding thistle *Carduus nutans*	Partial, good control in some areas	Minimal
Ragwort *Jacobaea vulgaris*	No other control required in most areas	Moderate
St John's wort *Hypericum perforatum*	No other control required in most areas	Ongoing (excellent)

In contrast to these successful programmes, a 10-year experiment removing mouse-ear hawkweed (*Pilosella officinarum* Vaill.) to simulate biocontrol showed very little vegetation change (Syrett et al. 2004), although more recent data from another study area on the Central Plateau of the North Island suggest the gall midge (*Macrolabis pilosellae*) is reducing mouse-ear hawkweed cover by 26% after 10 years and that other vegetation is replacing it (Landcare Research unpubl. data). Other ongoing monitoring programmes include long-term plots to measure changes in broom (Paynter et al. 2010b); detailed monitoring for tradescantia, which given the extensive ecological studies undertaken prior to the biocontrol programme should become the best studied biocontrol programme in New Zealand (Fowler et al. 2013); and a substantial research programme with the dual aims of evaluating the role of biocontrol in suppressing St John's wort and testing for population-level non-target effects on native *Hypericum* spp. (Groenteman et al. 2011; Landcare Research unpubl. data).

To complement these flagship monitoring studies we have developed some simple, cost-effective methods for end-users to evaluate the effectiveness of biocontrol. These include taking digital photos for quantitative analysis aimed at calculating changes in percentage cover of vegetation over time, and simple nationwide surveys of release sites to document changes in weed density. The strength of these approaches is the large number of sites from which data can be collected.

Cost-effectiveness

In Australia in 1998 the average cost of taking a weed biocontrol agent through to introduction was US$406,000 (McFadyen and Cruttwell 1998). This equated to NZ$910,601 in 2011 (taking into account the exchange rate of the day and CPI adjustment). In 2011 we estimated the average cost of developing agents over the previous decade for the National Biocontrol Collective to be NZ$393,000. This included the cost of developing agents subsequently rejected as unsuitable, and the cost of ancillary activities such as training workshops and presentations, and preparation of newsletters and other information resources. Some factors that have allowed Landcare Research to develop agents so cost-effectively include: the close relationship between operational research and government-funded research programmes; being able to take advantage of projects developed elsewhere or share costs with other players; and contractual arrangements that have allowed researchers to keep administration costs down and respond quickly to reshape projects, and redirect funds, when necessary.

Value of biocontrol

Economic data about the benefits of weed biocontrol to New Zealand have been lacking but efforts to gain this information are now beginning. Funding such retrospective studies has been difficult because funding agencies and end-users have preferred to use available resources to find new biocontrol agents instead. Also, the long-term nature of biocontrol means an economic analysis may not be appropriate until several decades after agents are released, and many New Zealand projects are still too young.

Recently an economic analysis has been undertaken for the St John's wort project (Landcare Research unpubl. data). When St John's wort beetles (*Chrysolina* spp.) were first released in the 1940s, the weed was spreading rapidly, particularly in high country pastures. By the 1980s, the beetles were successfully controlling the weed (Figure 5). Eco-climatic models were used to predict where the weed was capable of invading and to determine its potential range in the absence of any control. Only data from the South Island were used because the plant is a less serious problem in the North Island, and various filters were added to the model to create a realistic scenario. For example, the only areas of pasture included were those used for sheep, beef, and deer farming and where there was a high probability of St John's wort infestation. The model suggested 660 000 hectares of the South Island would have been badly infested if St John's wort had been allowed to grow uncontrolled until 2042. The negative impact

FIGURE 5 St John's wort beetles (*Chrysolina* spp.) forming a feeding front (centre) with stripped plants in their wake (left) and undamaged plants ahead (right). Inset: *Chrysolina quadrigemina*

from this level of infestation (based on loss of pasture and grazing to farmers) was calculated to be $109/ha with a smaller cost of $6/ha for manual weed control. The final figures suggested the net present value (NPV) of the introduction of the beetles, estimated over 70 years, is between $140 million (given a conservatively slow rate of spread) and $1,490 million (with a faster rate of spread). Therefore, the respective benefit-to-cost ratios are 10:1 and 100:1 and, even at the lower end, savings provided by the St John's wort biocontrol programme more than pay for all weed biocontrol programmes undertaken in New Zealand to date.

Financial gains from controlling environmental weeds such as mist flower are more difficult to determine because intrinsic benefits to native flora and fauna are not easily measurable in dollar terms. However, a preliminary analysis of the financial savings from no longer needing to control mist flower in the upper North Island suggests a cost reduction of $80,000–90,000 per year. The NPV for this is more than $3 million with a benefit-to-cost ratio of 2.5:1 – still very good over a 13-year period.

These examples indicate the substantial economic benefits to New Zealand already provided by weed biocontrol. In Australia, where many similar projects have been undertaken, a recent economic impact assessment of 104 years of weed biocontrol activity showed weed biocontrol has cost Australia on average $4.3 million per year but the estimated annual return from this investment is $95.3 million, a benefit-to-cost ratio of 23:1 (Page and Lacey 2006). However, not all biocontrol programmes are successful (although this is often because funding runs out before the work is finished) and Australia's huge annual return was produced by only 14 successful programmes. Nevertheless, while unsuccessful biocontrol programmes in Australia cost $15 million, this was insignificant compared with the benefits provided by successful ones. A surprising outcome from this study was that even a small reduction in a major widespread weed, e.g. 5% of lantana or blackberry, could more than pay for the cost of developing a biocontrol programme.

Excellent safety record

While some people still compare the introduction of weed biocontrol agents with the disastrous introduction of organisms like rabbits or ferrets, this comparison is specious: unlike the introductions of those mammals, weed biocontrol has an excellent safety record both in New Zealand and overseas. An analysis of past host-range testing (Fowler et al. 2004) and extensive surveys for damage to non-target plant species (Paynter et al. 2004; Waipara et al. 2009) show that host-testing, if undertaken appropriately, is a good indicator of what will happen in the field. Four insect species (St John's wort beetles, old man's beard leaf miner *Phytomyza vitalbae* Kaltenbach, and cinnabar moth) cause minor damage to native plants, which was predictable from host-testing. Conversely, the broom seed beetle (*Bruchidius villosus* F.) and gorse pod moth (*Cydia succedana* Denis and Schiffermüller) damaged non-target exotic plants closely related to the target weeds and this was not predictable from host-range testing; however, experimental studies showed that the past host-range testing of these two agents was not adequate and could have been improved by (1) increased replication, (2) including no-choice tests, i.e. without the normal host plant, and (3) releasing agents only from the same geographic populations as those tested (Haines et al. 2004; Paynter et al. 2008). These improvements now form part of standard best practice.

Less is known about non-target effects that occur when biocontrol agents become a food source for, or compete with, other species. Such 'ripple' or 'downstream' effects may be positive or negative; they are considered before biocontrol agents are released but are generally very difficult to predict accurately given the current level of knowledge of ecosystem functioning. However, research into food webs is underway, and we trust this will allow us to get better at predicting these indirect non-target effects (Fowler et al. 2012).

New facilities

The key role of weed biocontrol in New Zealand has been acknowledged by the construction of a new invertebrate containment facility at Lincoln in 2010 and a plant pathogen containment facility at Auckland in 2012. The plant pathogen containment facility is the first of its kind to be built in New Zealand and will streamline projects and make possible some that could not be undertaken without access to such a facility. Both new containment facilities offer natural light, which will improve success when working with some taxa such as rust fungi.

RESEARCH TO IMPROVE SUCCESS AND SAFETY

Despite the high establishment rate, over half the weed biocontrol agents established in New Zealand do not contribute to controlling their target weeds (Paynter et al. 2010a). We are investigating several possible reasons.

Host plant status

In some parts of New Zealand very low organic nitrogen levels (~1% dry weight) in heather appear to contribute to poor establishment of heather beetles (*Lochmaea suturalis* Thompson), possibly through an interaction between body size/fat reserves, overwintering survival and fecundity (Fowler et al. 2008).

Some accidentally arrived rusts in New Zealand – for example, blackberry rust and hieracium rust *Puccinia hieracii* var. *piloselloidarum* (Röhl.) H.Mart. – have failed to significantly suppress weeds; this may be a consequence of a poor match of the rust to the biotype of the plant. The development of quick and cost-effective molecular biology techniques is now allowing routine genetic studies of both hosts and potential agents so these mismatches can be avoided. These techniques also help identify the best areas of native ranges for surveys, and recent genetic studies of two new targets, pampas (*Cortaderia* spp.)

FIGURE 6 Molecular tools are proving invaluable with targets like pampas (*Cortaderia* spp.) that cannot be reliably identified using taxonomic features.

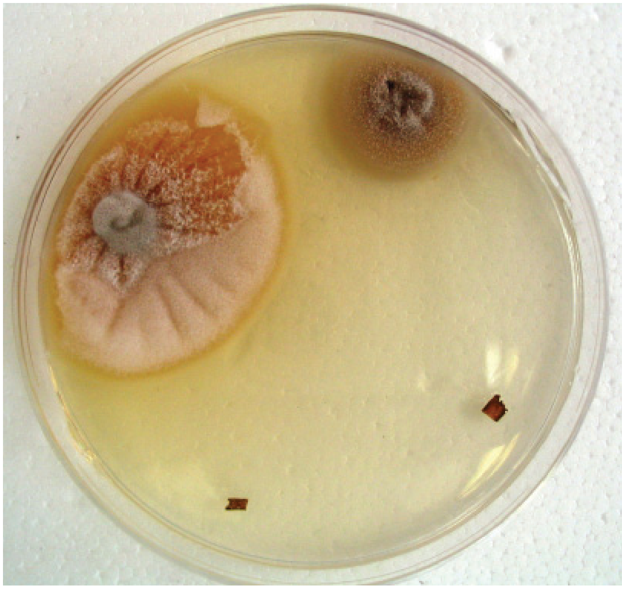

FIGURE 7 Endophytes found in old man's beard (*Clematis vitalba*) may explain poor success against this target to date. Understanding endophytes better may be the key to improving success rates.

and wild ginger (*Hedychium* spp.), have demonstrated their value. Traditional taxonomic features could not reliably distinguish various species of pampas (Figure 6) in the field, so the wrong host plants might have been surveyed (Landcare Research unpubl. data). The new techniques also showed that kahili ginger in New Zealand is a hybrid of two *Hedychium* species; this hybrid probably does not exist in the native range and therefore requires searching for slightly less host-specific agents (Landcare Research unpubl data).

All terrestrial plants have fungal endophytes, which may produce no visible symptoms. Evans (2008) proposed that endophytes could influence a weed's susceptibility to biocontrol agents, and we are testing this hypothesis with weeds like old man's beard and Californian thistle (Dodd et al. 2010). Until recently, most studies on endophytes involved identifying them by first isolating them into pure culture (Figure 7). This means species that grow very slowly or not at all in culture media were overlooked, while species that grew well in culture were over-represented. This bias can be partially overcome by direct amplification using target-specific primers on DNA extracted from surface-sterilised plant material (Porras-Alfaro and Bayman 2011), thus removing the need for culturing. Our current studies with Californian thistle tested the differences between culturing and direct amplification (using denatured gradient gel electrophoresis). The two methods complemented each other in their detection of overall fungal Ascomycota diversity, but only the DNA-based method detected fungi of the Basidiomycota, a group known to be difficult to culture (Dodd et al. 2010).

Climate match / seasonal phenology

Ragwort flea beetle (*Longitarsus jacobaeae* Waterhouse) and gorse spider mite (*Tetranychus lintearius* Dufour) perform poorly in higher rainfall regions (Hill et al. 1991; Gourlay et al. 2008), while poor seasonal synchrony reduces the impact of gorse pod moth (Paynter et al. 2008) and ragwort seed fly (*Botanophila jacobaeae* Hardy) (Dymock 1987). Recent modelling indicates the buddleia leaf weevil (*Cleopus japonicus* Wingelmüller) should be most effective against buddleia in warmer parts of New Zealand (Kriticos et al. 2009).

Agent interactions

Generally, combinations of control agents are required to control weeds, so agents must be chosen carefully to ensure their combined impacts will be additive – for example, see the laboratory study of gorse insects by Fowler and Griffin (1995). Without this care, one agent can negate the impact of another. For example, nodding thistle receptacle weevil (*Rhinocyllus conicus* (Froehlich)) and nodding thistle gall fly (*Urophora solstitialis* L.) were both released to predate seeds in nodding thistle heads, but the gall fly alone would likely destroy more seed than both agents destroy together (Groenteman et al. 2007). To avoid these kinds of effects, where a candidate agent might compete or otherwise interfere with an existing natural enemy of the weed, surveys to document and understand the suite of natural enemies already found on the weed in New Zealand are always undertaken at the start of new projects.

Synergistic interactions could be achieved via mutualisms in which insects vector plant pathogens. However, our research showed the old man's beard leaf miner is not a vector of the leaf fungus *Phoma clematidina* (Hill et al. 2004), and recent data suggest the Californian thistle stem miner *Ceratapion onorpordi* Kirby is not a significant vector of the rust *Puccinia punctiformis* (Str.) Röhl. (Cripps et al. 2009).

Mutualisms may influence weed biocontrol in other ways. For example, although it has been assumed that seed-feeders rarely destroy enough seed to affect weed populations, Paynter et al. (2010b) predicted that the impact of the broom seed beetle could be enhanced by reducing the abundance of pollinators; this could be achieved by keeping bee hives well away from targeted stands of broom.

Natural enemies

Although predation is known to reduce the effectiveness of gorse spider mite in New Zealand (Peterson et al. 2000), the effect of predators on weed biocontrol agents in New Zealand is not well understood and is an area of continuing research.

However, a recent study of parasitism of weed biocontrol agents in New Zealand has shown this is not a major cause for alarm (Paynter et al. 2010a). While parasitism may have reduced the efficacy of about 20% of agents released here, it has not affected the overall outcome of weed biocontrol programmes because control has still been achieved by other, unaffected agents. We also found that species with many parasitoids in their native range are more likely to pick up a large number here, and that agents with a native equivalent here (i.e. a native insect closely related to the agent and occupying a similar feeding niche on the target weed or a closely related native plant in New Zealand) are also more likely to be parasitised. This means we can now select agents least likely to be parasitised, thereby minimising the chances of unwanted 'downstream' effects and wastage of resources.

We are also researching the impacts of pathogens on the performance of insect biocontrol agents. This research began after we encountered problems with a microsporidian and gregarine parasites in chrysomelid beetles. With heather beetle, rearing iso-female lines (offspring from a single field-collected female), surface sterilisation of beetle eggs, and frequent testing resulted in cultures free from an unidentified microsporidian (Wigley 1997). However, this approach, combined with very poor establishment of field-released beetles, has resulted in a genetically bottlenecked population that may be compromising the heather beetles' performance as a biocontrol agent in New

Zealand (Fowler et al. 2008). Heather beetle populations are free from the microsporidian in New Zealand (Peterson et al. 2004) but in the United Kingdom this pathogen is present in field populations; consequently, importing more heather beetles to restore heterozygosity carries the risk of accidentally importing the disease. Detecting the pathogen is currently difficult because light microscopy often fails to detect low levels of the microsporidian. Therefore, we are developing more sensitive molecular techniques to improve detection before considering any potential importation and release of new genetic material.

The first insect agent approved for release against tradescantia was the leaf beetle *Neolema ogloblini* F. Routine screening of this beetle revealed high levels of a gregarine (sporozoan protozoan) gut parasite. This appeared to reduce beetle fecundity, longevity and general vigour, and therefore potentially compromised its biocontrol efficacy. Attempts to obtain a gregarine-free population of the leaf beetle saw 2 years of increasingly intensive methods, including using highly hygienic field collection methods in Brazil to get clean material at source, surface sterilisation of eggs, cages with HEPA-filtered air in containment, and attempts to improve our gregarine detection methods by gut dissection and DNA probes (both of which proved less easy and more expensive than anticipated). Success was eventually achieved by repeated subculturing. First, eggs were collected as hygienically as possible from single female beetles (each having been paired with a single male). Then, each larva was reared in isolation but with poor hygiene to ensure any low level of gregarine infection would be expressed sufficiently to minimise the risk of getting false negatives in subsequent testing. All apparently infected lines were eliminated. Finally, in an attempt to restore lost heterozygosity and overcome any inbreeding depression or adaptation to laboratory conditions, lines were crossed before they were released from containment.

Refinements to host range testing

A recent case study demonstrated that if modern safety standards had been applied we would have rejected the St John's wort beetles for release in New Zealand on the grounds of a high risk of long-term non-target effects (Groenteman et al. 2011). However, the high degree of damage in the retrospective host range tests does not appear to eventuate in naturally occurring populations of indigenous *Hypericum* species. In conjunction with our current understanding of the economic benefits of St John's wort biocontrol in New Zealand (see *Value of biocontrol* above) this finding emphasises the downsides of rejecting effective and essentially safe agents due to false-positive results from artificial test conditions in containment. Work is currently being undertaken to identify the type of ecological knowledge that might be obtained before agents have established in the field, and that could better inform decisions to accept or reject potentially effective agents when they utilise non-target hosts under test conditions.

Selecting targets

With so many weeds to manage and given the inevitability of limited resources, targets must be prioritised carefully. Recently, we have developed a decision framework that allows us to identify likely 'winners' and difficult weed biocontrol targets, both with a surprising degree of confidence (Paynter et al. 2009 unpubl. report). This ranking system incorporates measures of the weed's impact (importance), the likelihood of successful biocontrol (feasibility), and the likely effort (cost).

Determining the scores for feasibility and cost of biocontrol for each weed required several steps. A dataset compiled from weed biocontrol programmes worldwide has allowed us to identify the factors that have the greatest influence on the cost and impact of biocontrol. For example, factors that will increase the likely cost of a biocontrol programme include conflicts of interest that could foster opposition to controlling the weed, and whether the weed has valued close relatives. Conversely, costs will decrease if the weed is the target of a biocontrol programme elsewhere, because research into natural enemies has already been conducted and damaging biocontrol agents identified. Examples of factors likely to increase the impact of biocontrol on a weed include clonal rather than sexual reproduction, and being an aquatic or wetland species, whereas biocontrol is likely to have less impact if the plant is a major rather than an uncommon weed in its home range. Many other factors have been suggested as possibly important (e.g. susceptibility to secondary disease) but data for these are inadequate so they are not included in the current prioritisation framework; however, they may be added as refinements in the future.

It is also important to get the right balance between targeting the most important weeds and targeting the best biocontrol targets. These are not always the same. Some pragmatic decision-making will always be needed when deciding what biocontrol projects to invest in, and ultimately the projects that go ahead are those that people are prepared to fund. Funding decisions are based on many factors, including politics, regional needs, previous investment and timing, as well as science.

FUTURE ISSUES/CHALLENGES

Improved rearing/establishment

Despite a high rate of establishment of agent species, some released species have proved difficult or impossible to establish. In particular, several agents that appeared to be very promising in terms of potential impact on weeds like hawkweed and old man's beard failed to establish. As well as representing a failed investment by stakeholders, both these weeds have few potential agent species in the native range, so the failure of these recalcitrant agents to establish is impacting on possible success of the biocontrol programmes against these weeds.

Releases of heather beetle (see above) also came close to complete failure with only one out of 17 releases establishing. Beetles collected from this population were released at many high altitude sites on the Central Plateau of North Island, where heather infestations are most serious, but they resulted in a similarly poor rate of establishment. In marked contrast, when we released beetles at lower altitudes in smaller heather infestations near Rotorua, every population established. This appears to be the result of more benign winter and spring weather and higher nitrogen levels in the host plant than at the high altitude sites. In hindsight, if we had released some of the original iso-female lines in 1996–1998 at these lower altitude sites we would probably not have ended up with the currently genetically bottlenecked population of heather beetle in New Zealand. Fertilising release sites in the Central Plateau also appears to be improving beetle establishment (Landcare Research unpubl. data).

Given the risk of small populations failing to establish, releasing agents at the best sites for establishment may be a better strategy than releasing them immediately into the areas where the weed is worst. This might maximise the chance of establishing otherwise recalcitrant agents, thereby providing well-established populations that can be used for later collection and release into the more challenging sites. Alternatively, sites in challenging regions could be manipulated to improve the likelihood of establishment: for example, by irrigating, caging (to exclude predators or limit severe frosts), or fertilising to improve host plant quality. In the past we used climate data from the weather station nearest to an agent or weed population, but these data do not always reliably reflect local conditions; consequently, we are now using data-loggers at the collection sites for the agents in their native ranges and in the areas where the weed is a problem in New Zealand, to test whether there is a climate mismatch. For example, the dramatic diurnal fluctuations in temperature at high altitude sites on the Central Plateau may contribute to the low establishment rate of heather beetles (Peterson et al. 2011 unpubl. report).

More for less

With hundreds of weed species to manage already, and the expectation that the number will continue to increase as species continue to naturalise and move out of lag phases, biocontrol will need to be developed more quickly than in the past. Where a taxonomic group of target weeds is unrelated to either the New Zealand indigenous flora or valued exotic plants such as crops or ornamentals, we are increasingly exploring a multi-targeting approach, where biocontrol agents with a broader range of hosts are introduced to target a group of related weed species (Groenteman et al. 2008). For example, the green thistle beetle (*Cassida rubignosa* Muller) has recently been released and established in the hope it might damage all currently weedy thistle species and prevent the many additional thistle species that are currently not weedy from ever becoming so (Figure 8). Multi-targeting will usually require in-depth studies of the ecology and population dynamics of the target weeds and possible agents, and might therefore only be warranted where a significant number of weeds could be potentially controlled.

New targets

Biocontrol appears to be underutilised as a method for controlling aquatic weeds in New Zealand. Excluding wetland species that are normally only flooded for part of their life cycle, 52 aquatic species have naturalised and become weeds, but so far only one, alligator weed, has been the subject of attempted biocontrol – and with some success. The prioritisation project described above found that aquatic species appear more susceptible to biocontrol than terrestrial weeds, and many of the worst aquatic weed species in New Zealand appear likely to be good targets for biocontrol (Landcare Research unpubl. data). Consequently, we hope biocontrol programmes can be developed in the near future for the three species deemed of highest importance by key stakeholders: lagarosiphon (*Lagarosiphon major* (Ridl.) Moss ex Wager), hornwort (*Ceratophyllum demersum* L.), and egeria (*Egeria densa* Planch.).

FIGURE 8 The green thistle beetle (*Cassida rubiginosa*) has been released with the aim of tackling all thistles in New Zealand. Such a multi-targeting approach may need to be used increasingly in the future. Photo J. Bythell.

Weeds are also a huge and growing problem for Pacific Island nations and territories. Biocontrol using agents developed elsewhere has already met with some success in the Pacific, but many more programmes are needed (Julien et al. 2007). These small nations and territories lack the capability, resources and infrastructure to develop their own weed biocontrol programmes (Dovey et al. 2004). However, New Zealand is now well placed to assist in the development of biocontrol programmes for the wider Pacific, if funding can be found, especially with the recent construction of a plant pathogen containment facility in Auckland.

Loss of other control measures

In many countries use of herbicides is becoming increasingly constrained because weeds are becoming resistant, products are being removed from sale following re-evaluation, rules governing usage are being tightened, and the public is demanding more organic produce free from chemical residues. Some countries, like Canada, have responded by investing heavily in the development of biopesticides (Bailey et al. 2010), but in New Zealand some limited work to develop biopesticides for weeds has not yet resulted in any commercially available products (Fröhlich et al. 2000). The long time frames for development, high costs of producing products that may have relatively small markets, and the technical challenges that need to be overcome to allow biopesticides to be easily and reliably used all constrain their development (Glare et al. 2012).

However, the need for more environmentally friendly, sustainable pest control products will continue to increase, so further investment in this area of research will be essential. This is especially relevant in sensitive environments such as water catchments, where a portion of all herbicides applied to forests, croplands, roadsides and gardens is inevitably lost to water bodies, either directly through runoff or indirectly by leaching through groundwater into ephemeral streams or lakes (Graymore et al. 2001). To address this issue, research is currently being undertaken into the possible use of silver leaf fungus (*Chondrostereum purpurerum* (Pers.) Pouzar) as an alternative to synthetic herbicides for control of trees like willow (*Salix* spp.) and poplar (*Populus* spp.) in riparian areas (Bellgard et al. 2012).

Climate change implications

Climate change does not seem to be a major concern for weed biocontrol. A recent study considered the implications for the ragwort biocontrol programme under likely climate change scenarios, focusing especially on whether current successful control could break down (Gerard et al. in press). We expect that if weeds are able to change their distributions, their biocontrol agents will simply follow, because the weed and the agent will have similar climatic requirements. Also, agents can now be selected with future conditions in mind. Warmer temperatures and fewer frosts may even suit some biocontrol agents; conversely, more extreme events like droughts (especially if they occur in spring rather than late summer) could make biocontrol of difficult targets like hawkweeds (*Pilosella* spp., *Hieracium* spp.) even more difficult.

Increased carbon dioxide in the atmosphere is expected to increase plant productivity and lead to increased biomass but of lower nutritional value because the amount of nitrogen in the plant material will decrease. Lower plant quality could mean that biocontrol agents perform worse; conversely, agents might damage plants more heavily in order to get the nutrition they require. The seasonal phenology of plants is also likely to change. This could also be good or bad depending on whether it disrupts current good synchronisation of agents with their hosts (e.g. the broom psyllid (*Arytainilla spartiophila* Forster) with bud burst of broom in the spring), or better aligns agents that are not currently well synchronised (e.g. gorse pod moth with flowering and pod production of gorse). Such interactions can be monitored and, if necessary, additional agents sought.

Unquestionably, the key priority for planning in New Zealand is the likely worsening of problems caused by weed species not currently under biocontrol. Even without the exacerbating effects of climate change, weeds will become increasingly problematic as more species naturalise or move out of lag phases. Add the effects of climate change and we can expect even more weed species to naturalise and to extend their ranges, such as those currently limited by frosts. Some of these new weed problems may be able to be nipped in the bud by improved surveillance, or neutralized in pre-emptive strikes by releasing biocontrol agents with wider host-ranges for this purpose.

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