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Predictability of pathogen host range in classical biological control of weeds: an update

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Abstract Before an exotic pathogen can be released as a classical biological control agent the likely positive and negative outcomes of that introduction must be predicted. Host range testing is used to assess potential damage to non-target plants. To-date 28 species of fungi have been released as classical biological control agents against weeds world-wide. These pathogens have been reported infecting only six non-target plant species outdoors and all of these incidents were predicted. Many more non-target plant species developed disease symptoms in glasshouse tests than in the field. Consequently, data from other sources are needed to ensure potential agents are not prematurely rejected. Predictions of pathogen host range to date have been sufficiently accurate to prevent unpleasant surprises. Exotic pathogens are a safe and useful tool for weed control, especially in natural areas rich in valued non-target species.

Keywords Biological control · Pathogen · Host range · Cost:benefit ratio · Natural ecosystems

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Introduction

Plant pathogens are an excellent tool for the control of exotic plants that have invaded natural areas. Other tools, e.g. herbicides and physical removal, often have negative impacts on non-target organisms and this can be particularly problematic in natural areas that are rich in valued, mostly native, non-target plants. Many pathogens are extremely host-specific and capable of damaging a target weed without disturbing other vegetation nearby. Also, pathogens with wind-borne spores can reach weeds in remote and inaccessible natural areas where it would be physically difficult and/or prohibitively expensive to apply other methods of control.

For example, in New Zealand, the weed mist flower (*Ageratina riparia* (Regel) R. King and H. Robinson, Asteraceae) invades native forests and forms dense mats of semi-woody stems that smother native plants. If herbicide were applied in this situation the natives would be killed along with the weed and the weed would then recover faster than many of the desirable plants, potentially leading to a worsening of the situation. For herbicide to be effective there would need to be follow up spraying over a number of years to reduce the seed bank of mist flower (Tony McCluggage, personal communication) and that is a costly option. Also, mist flower can tolerate some shading and it spreads along riverbanks with the result that it can grow in remote and inaccessible areas of native forest where it is difficult to manage (personal observation).

Consequently, two highly specific classical biological control agents were introduced to New Zealand: a white smut fungus: *Entyloma ageratinae* Barreto and Evans (Ustilaginomycetes) and a gall fly: *Procecidochares alani* Steyskal (Tephritidae). These agents successfully reduced the density of mist flower infestations without harming any non-target plants (Barton et al. 2007). As a result the species diversity of native plants in monitored plots recovered (as mist flower cover decreased) until it was at a similar level to that in plots that remained free of the weed (Barton et al. 2007). The smut fungus spread very quickly (at least 80 km in two years) and infected even small, apparently isolated patches of the weed (Barton et al. 2007). Thus, these highly specific agents were very beneficial to the conservation of native plants in a natural ecosystem.

The key to positive outcomes such as this is to accurately predict the field host range of the potential classical biological control agents so that the risks they pose to non-target plants can be accurately weighed up against potential benefits. In this paper the terms 'costs' and 'benefits' will be used in an all-encompassing way. 'Costs' include not just monetary losses but also potential negative impacts on: the health of non-target organisms, biodiversity, environmental services, and political/public goodwill. Likewise, benefits include monetary savings (e.g. through less herbicide use) but also positive impacts on the heath and vigour of desirable plants (native and exotic) and the other organisms that interact with them (including humans).

Given that it will only ever be possible to test a sub-set of the non-target plants that a biological control agent could encounter in the field, it is essential that this sub-set is carefully chosen. Plant pathologists are fortunate in that Wapshere's 'centrifugal phylogenetic method' for choosing test plants (Wapshere 1974) was developed just at the time when biological control of weeds with pathogens began. Basically, this method states that the non-target plants most likely to be attacked by a proposed biological control agent are the closest relatives of its known host(s). Since the target weed is invariably a known host, test lists should be weighted with plants in the same genus, sub-family and family as the weed, especially those that grow where the pathogen will be used (Wapshere 1974). The methods used for host range testing, and the importance placed on various types of non-target plants, have changed over time. However, when it comes to choosing test plants pathologists have stuck with Wapshere's method and have been rewarded with useful data. This issue is discussed further in Barton (née Fröhlich) (2004). Note that molecular techniques are very quickly improving our phylogenetic knowledge of plant relationships, and that that is helping to ensure that test lists include appropriate species (e.g. Berner 2010).

The ability of researchers to predict the field host range of fungal pathogens to be used for classical biological control was assessed in Barton (née Fröhlich) (2004). The purpose of this paper is to briefly summarise the information provided previously and to update it. In the process, the author hopes to show that if pathogens continue to be used judiciously, the benefits of their use as classical biological control agents in natural areas should far outweigh the costs.

Overall comparison of 'pre' and 'post'-release host ranges

All of the fungi which have been released as classical biological control agents for weed to date (to the authors' knowledge) are listed in Table 1. This table is an updated version of one published in Barton (née Fröhlich) (2004). Note that full Latin names and authorities of target weeds and pathogens discussed in this paper are given in Table 1 rather than in the text. Information on events that have occurred between the date when the original paper was compiled (February 2003) and the present (April 2011) was obtained by contacting the researchers who provided data for the earlier paper (via e-mail) and asking them for relevant information. Note also that almost all of the information in Table 1 about non-target damage outdoors came from unpublished sources (personal communications). There have been deliberate searchers for non-target damage conducted recently in New Zealand and Papua New Guinea (see case studies 4 and 5 below for details) but these remains the exception rather than the rule for reasons given in Barton (née Fröhlich) (2004) and Hopper (2001).

For the purposes of this paper, a biological control 'project' is defined as the use of one species of pathogen to control one weed (or several closely related weeds) in a single country. Using that definition

Table 1 Fungal pathogens introduced as classical biological control agents of exotic weeds

Exotic weed	Fungal pathogen	Country of origin	Country (date) of introduction	No. non-target spp. included in indoor HR testing	No. non-target spp. damaged in indoor HR testing	No. non-target spp. damaged outdoors (source of information)	References to information re. HR testing
**Acacia saligna* (Labill.) H. L. Wendl. (Mimosaceae)	*Uromycladium tepperianum* (Sacc.) McAlpine (Uredinales: Pileolariaceae)	Australia	South Africa (1987)	47	6	2 (M. J. Morris, A. Wood and J. Hoffmann, pers. comm.)	Morris (1987)
Ageratina adenophora (Spreng.) R. M. King & H. Rob. (Asteraceae)	*Phaeoramularia eupatorii-odorati* (J. M. Yen) X. J. Liu & Y. L. Guo (hyphomycete)	Mexico	South Africa (1987)	8	0	0 (M. J. Morris, pers. comm.)	Morris (1989)
Ageratina riparia (Regel) R. M. King & H. Rob. (Asteraceae)	*Entyloma ageratinae* R. W. Barreto & H. C. Evans (Entylomatales: Entylomataceae)	Jamaica	Hawaii, USA (1975) South Africa (1989) New Zealand (1998)	Hawaii 44 South Africa 18 New Zealand 34 Includes 1 sp. tested in all 3 countries and 1 sp. tested in 2 of 3 countries	Hawaii 0 South Africa 1 New Zealand 1 (same 1 in SA & NZ)	Hawaii 0 (E. M. Killgore and E. E. Trujillo, pers. comm.) South Africa 0 (M. J. Morris, pers. comm.) New Zealand 0 (personal observation)	Morin et al. (1997), Fröhlich et al. (1999)
**Asparagus asparagoides* (L.) Druce (Asparagaceae)	*Puccinia myrsiphylli* (Thüm) G. Winter (Uredinales: Pucciniaceae)	South Africa	Australia (2000)	42	0	0 (L. Morin, pers. comm.)	Morin (1999), Morin et al. (2002)
Baccharis halimifolia L. (Asteraceae)	*Puccinia evadens* Harkn. (Uredinales: Pucciniaceae)	USA	Australia (1997)	94[a]	4[a]	0 (A. J. Tomley, pers. comm.)	A. J. Tomley (pers. comm.), Verma et al. (1996)
**Carduus thoermeri* Weinm. (Asteraceae)	*Puccinia carduorum* Jacky (Uredinales: Pucciniaceae)	Turkey	USA (1987)	63[a]: 6[a] 2 tests, 1 spp. in both	16: 1 1 sp. damaged in both tests	1[b] (Baudoin et al. 1993)	Baudoin et al. (1993), Politis et al. (1984), Bruckart (2005)
Carduus pycnocephalus L. *Carduus tenuiflorus* Curtis (Asteraceae)	*Puccinia cardui-pycnocephali* P. Syd. & Syd. (Uredinales: Pucciniaceae)	Italy France	Australia (1993)	45	1	0 (E. Bruzzese and J. J. Burdon, pers. comm.)	Burdon and Thrall (2002), Evans (2000)

Table 1 continued

Exotic weed	Fungal pathogen	Country of origin	Country (date) of introduction	No. non-target spp. included in indoor HR testing	No. non-target spp. damaged in indoor HR testing	No. non-target spp. damaged outdoors (source of information)	References to information re. HR testing
**Centaurea solstitialis* L. (Asteraceae)	*Puccinia jaceae* var. *solstitialis* (Uredinales: Pucciniaceae)	Turkey	USA (2003)	56[a]: 11[a] 2 tests, 7 spp. in both	11	0 (W. L. Bruckart III, pers. comm.)	Bruckart (1989, 2006)
Chondrilla juncea L. (Asteraceae)	*Puccinia chondrillina* Bubák & P. Syd. (Uredinales: Pucciniaceae)	Italy Turkey	Australia (1971, 1980, 1982, 1996) USA (1976) Argentina (1982)	Australia 58[a] USA 1[a] Argentina N/A	Australia 0 USA 0 Argentina N/A	Australia 0 (L. Morin, pers. comm.) USA 0 (D. B. Joley and D. Woods, pers. comm.) Argentina 0 (H. A. Cordo, pers. comm.)	Hasan (1972), Cullen et al. (1973), Emge et al. (1981), H. A. Cordo (pers. comm.)
Clematis vitalba L. (Ranunculaceae)	*Phoma clematidina* (Thüm.) Boerema (coelomycete)	USA	New Zealand (1996)	69: 57[a] 2 tests, 17 spp. in both	7: 42[a,c]	0 (A. G. Spiers, pers. comm.)	Spiers (1995, 1996)
Clidemia hirta (L.) D. Don (Melastomataceae)	*Colletotrichum gloeosporioides* f.sp. *clidemiae* E. E. Trujillo, Latterell, A. E. Rossi (coelomycete)	Panama	Hawaii, USA (1986)	11[d]	0	0 (E. E. Trujillo, pers. comm.)	Trujillo et al. (1986)
Cryptostegia grandiflora Roxb. ex R. Br. (Asclepiadaceae)	*Maravalia cryptostegiae* (Cummins) Y. Ono (Uredinales: Chaconiaceae)	Madagascar	Australia (1994)	71	3[a]	0 (H. C. Evans, pers. comm.)	Evans and Tomley (1994)
Eichhornia crassipes (Mart.) Solms (Pontederiaceae)	*Cercospora piaropi* Tharp (hyphomycete)	USA	South Africa (1991)	57	4[a]	0 (M. J. Morris, pers. comm.)	Conway and Freeman (1977), Morris et al. (1999)
Galega officinalis L. (Fabaceae)	*Uromyces galegae* (Opiz) Sacc. (Uredinales: Pucciniaceae)	France	Chile (1973)	14[a]	0	0 (R. W. Barreto, pers. comm.)	Oehrens and Gonzalez (1975)
Heliotropium europaeum L. (Boraginaceae)	*Uromyces heliotropii* Sred. (Uredinales: Pucciniaceae)	Turkey	Australia (1991)	90[a]	4	0 (L. Morin, pers. comm.)	(Hasan et al. 1992)

Table 1 continued

Exotic weed	Fungal pathogen	Country of origin	Country (date) of introduction	No. non-target spp. included in indoor HR testing	No. non-target spp. damaged in indoor HR testing	No. non-target spp. damaged outdoors (source of information)	References to information re. HR testing
Hieracium pilosella L. (Asteraceae)	*Puccinia hieracii* var. *piloselloidarum* (Probst) Jørst. (Uredinales: Pucciniaceae)	Europe Ireland	New Zealand (1995) New Zealand (1998)	N/A[e] 124[a]	N/A 0[f]	0 (Jenkins 1998) 0 (T. Jenkins, pers. comm.)	Jenkins (1996)
Lantana camara L. (Verbenaceae)	*Septoria* sp. (coelomycete) and *Prospodium tuberculatum* (Speg.) Arthur (Uredinales: Uropyxidaceae)	Ecuador Brazil	Hawaii, USA (1997) Australia (2001)	16[a] 53	*Septoria* 0 *Prospodium* 0	*Septoria* 0 (E. E. Trujillo, pers. comm.) *Prospodium* 0 (A. J. Tomley, pers. comm.)	Trujillo and Norman (1995) Barreto et al. (1995)
Miconia calvescens DC. (Melastomataceae)	*Colletotrichum gloeosporioides* f. sp. *miconiae* Killgore & L. Sugiy. (coelomycete)	Brazil	Hawaii, USA (1997) Tahiti, French Polynesia (2000)	28[d]	Hawaii + Tahiti 0	Hawaii 0 (E. M. Killgore, pers. comm.) Tahiti 0 (J.-Y. Meyer, pers. comm.)	Meyer and Killgore (2000), Killgore et al. (1999)
**Mikania micrantha* H.B.K. (Asteraceae)	*Puccinia spegazzinii* de Toni (Uredinales: Pucciniaceae)	Trinidad and Tobago and Peru (India) Argentina (China) Ecuador (Taiwan, Fiji & PNG)	India (2005) China (mainland) (2006) Taiwan (2008) Fiji & Papua New Guinea (2009)	India 59[a]: 56[a] 2 tests, 18 spp. in both China & Taiwan 59[a]: 64[a] 2 tests, 8 spp. in both Fiji & PNG 59[a]: 11 2 tests, 8 spp. in both	All countries: 4	India 0 (C. A. Ellison, pers. comm.) China & Taiwan 0 (C. A. Ellison and S. S. Tzean, pers. comm.) Fiji 0 (A. Kawi, pers. comm.) PNG 1 (C. A. Ellison and M. Day, pers. comm.)	Ellison et al. (2008), Ellison and Day (2010), C. A. Ellison and S. S. Tzean (pers. comm.)

Table 1 continued

Exotic weed	Fungal pathogen	Country of origin	Country (date) of introduction	No. non-target spp. included in indoor HR testing	No. non-target spp. damaged in indoor HR testing	No. non-target spp. damaged outdoors (source of information)	References to information re. HR testing
Mimosa pigra L. (Mimosaceae)	*Diabole cubensis* (Arthur & J. R. Johnst.) Arthur (Uredinales: Raveneliaceae) and *Sphaerulina mimosae-pigrae* H. C. Evans & G. Carrión (Mycosphaerellales: Mycosphaerellaceae) (anamorph = *Phloeospora mimosae-pigrae* H. C. Evans & G. Carrión, coelomycete)	Mexico Mexico	Australia (1996) Australia (1994)	71 104	*Diabole cubensis* 1[g] *Sphaerulina mimosae-pigrae* 0	*Diabole cubensis* 0 (B. Hennecke, pers. comm.) *Sphaerulina mimosae-pigrae* 0 (B. Hennecke, pers. comm.)	Evans (2000), Seier and Evans (1996), M. K. Seier (pers. comm.), Forno et al. (1996), Seier and Evans (1996), M. K. Seier (pers. comm.)
Myrica faya Aiton (Myricaceae)	*Septoria hodgesii* D. E. Gardner (coelomycete)	USA (N. Carolina)	Hawaii, USA (1997)	21[d]	0	0 (D. E. Gardner and E. M. Killgore, pers. comm.)	Gardner et al. (1999)
Parthenium hysterophorus L. (Asteraceae)	*Puccinia abrupta* var. *partheniicola* (H. S. Jacks.) Parmelee (Uredinales: Pucciniaceae) and *Puccinia melampodii* Dietel & Holw. (Uredinales: Pucciniaceae)	Mexico Mexico	Australia (1991) Australia (1999)	89[a] 63[a]	*P. a.* var. *Partheniicola* 1 *P. melampodii* 6[a]	*P. a.* var. *Partheniicola* 0 (H. C. Evans and A. J. Tomley, pers. comm.) *P. melampodii* 1[b] (H. C. Evans and A. J. Tomley, pers. comm.)	Parker et al. (1994), Evans (2000), M. K. Seier (pers. comm.)
Passiflora tarminiana Coppens & V. E. Barney (Passifloraceae)	*Septoria passiflorae* Syd. (coelomycete)	Colombia	Hawaii, USA (1996)	6[d]	1	0 (E. E. Trujillo, pers. comm.)	Trujillo et al. (1994)
Rubus constrictus Lefev. & P. J. Muell. *Rubus ulmifolius* Schott (Rosaceae)	*Phragmidium violaceum* (Schultz) G. Winter (Uredinales: Phragmidiaceae)	Germany	Chile (1973)	2	0	0 (R. W. Barreto, pers. comm.)	Oehrens and Gonzalez (1977)

Table 1 continued

Exotic weed	Fungal pathogen	Country of origin	Country (date) of introduction	No. non-target spp. included in indoor HR testing	No. non-target spp. damaged in indoor HR testing	No. non-target spp. damaged outdoors (source of information)	References to information re. HR testing
**Rubus fruticosus* agg.	*Phragmidium violaceum*	Europe France France	Australia (1984) Australia (1991) Australia (2004)	N/A[e] 51[a,h]: 7 2 tests, 7 spp. in both 6[a] 3rd test on 8 new isolates, 0 spp. tested previously	N/A 6[a]: 7 1[i]	1 (in New Zealand) (J. Barton, pers. obs.)	Bruzzese and Hasan (1986a), Morin and Evans (2003)
Ulex europaeus L. (Fabaceae)	*Uromyces genistae-tinctoriae* f. sp. *ulicis* MacDon. (Uredinales: Pucciniaceae)	Scotland	Hawaii, USA (2000)	35	2	0 (E. M. Killgore, pers. comm.)	Killgore and Sugiyama (1996)

* This table is an updated version of the one given in Barton (née Fröhlich) (2004). Lines marked with an asterisk have new or altered information

HR host range

[a] This total is for 'species,' more than one 'variety' of at least one species was tested and/or damaged by the fungus

[b] Damaged species was planted in a test plot outdoors

[c] Of the 17 species included in both sets of host range tests: four spp. had no symptoms in either set of tests; six spp. had symptoms in both sets of tests; six spp. had no symptoms in test 1 but did have symptoms in test 2; and, 1 sp. had symptoms in test 1, but not in test 2

[d] This test list was unusually short because there are no native members of the target plant's family in the area to which the biological control agent was introduced

[e] *Puccinia hieracii* and *Phragmidium violaceum* both appeared some years before their official releases. The first isolates were therefore not subject to host range tests

[f] Species in the same genus and subgenus as the target weed were not included in official host range testing, even though it was known from the literature and unpublished work that they might be susceptible to infection, because they were considered target species

[g] While no species additional to the target weed were damaged, a variety of the target species, additional to the target variety, was susceptible

[h] Because there are many commercially important *Rubus* hybrids, many varieties of the 51 species were included in testing (108 taxa in total)

[i] One of the *Rubus* taxa that was resistant to the original pool of *P. violaceum* isolates tested was found to be susceptible to new isolates of the rust

there have been 38 such projects worldwide (Table 1). These projects involved 28 species of pathogens, all of them fungi. About 28 weeds or weed complexes were targeted. The pathogens used as agents originated in 18 different countries and were released in 11 countries. More than half of them have reduced populations of their target weed(s) (Charudattan 2005) but their success (or otherwise) will not be discussed further here.

Information in the above table that is additional, or different to, that presented in a similar table in Barton (née Fröhlich) (2004) is provided for the following weeds/pathogens:

Acacia saligna/Uromycladium tepperianum: See case study 3 below.
Asparagus asparagoides/Puccinia myrsiphylii: The country of origin of the pathogen was recorded previously as Brazil. It is actually South Africa (author error).
Carduus thoermeri/Puccinia carduorum: See case study 1 below.
Centaurea solstitialis/Puccinia jaceae var. *solstitialis*: Pathogen was released after data in the previous paper was compiled.
Mikania micrantha/Puccinia spegazzinii: Pathogen was released after data in the previous paper was compiled. Also, see case study 5 below.
Rubus fruticosus/Phragmidium violaceum: See case study 4 below.

Non-target damage has been reported outdoors in only five of the 38 projects worldwide (Table 1). In the remaining 33 projects, the pathogen released has either not established or has only been found on the target weed(s) since release. Note that there were 14 projects in which the target weed was the only plant damaged by the proposed agent in pre-release testing. In all of these cases, there was no non-target damage observed in the field (Table 1).

Two of the five cases of non-target damage outdoors were recorded during outdoor host range tests, so there are only three cases of disease symptoms on non-target plants in natural areas. All three cases were predicted by pre-release host range testing. That is, the non-target plants infected by the biological control agents were rated as 'susceptible' to that agent in indoor host range tests. In all three cases a decision was made to release the agent anyway because potential benefits were seen to outweigh potential costs. The details of all five 'projects' in which non-target plants were damaged outdoors are given below. Note that the first three of the five were discussed at length in Barton (née Fröhlich) (2004) and so only a summary and some new information are provided here.

Case studies

1. Biological control of *Carduus thoermeri* (nodding or musk thistle) with *Puccinia carduorum* (rust)

Musk thistle (=*C. thoermeri* although sometimes also referred to as *Carduus nutans* L. ssp. *leiophyllus* (Petrovic) Stoj. & Stef.) is native to Europe and Asia but became a major problem in pastures and rangelands in the USA where it competes with more desirable species (Baudoin et al. 1993). The rust fungus *Puccinia carduorum* was selected as a potential classical biological control agent and it was applied to 63 non-target species in the Asteraceae family to test its host range (Politis et al. 1984). Researchers found that the target weed was the only plant that suffered severe disease symptoms, however in the glasshouse some symptoms were also observed on 16 non-target species, including globe artichoke (which is grown commercially in the USA) and some thistles that are native to America. All the plants that developed disease symptoms were in the same tribe as the target weed (Politis et al. 1984).

The development of disease symptoms on globe artichoke in the glasshouse could have led to the rejection of *P. carduorum* as a biological control agent. However, fortunately it was known that in Eurasia it is not uncommon for globe artichokes to grow near musk thistle plants infected by *Puccinia carduorum* yet artichoke had never been recorded as a host of the rust there (Bruckart et al. 1985). Because of this contradiction between glasshouse results and field observations, the researchers were given permission to test the rust outdoors in the USA, outside of containment. This situation, i.e. the release of a pathogen in the field in a new area with the intention of eradicating it if it attacked non-target species outdoors, is probably unique in the history of biological control of weeds with pathogens.

The outdoor trial was conducted over two years and the plants tested were globe artichoke (*Cynara scolymus*) and ten species of native American thistles (*Cirsium* species) (Baudoin et al. 1993). The trial was conducted in an area of Virginia without large stands of musk thistle so as to facilitate eradication of the rust if results of the tests were unfavourable (Baudoin et al. 1993). Over the whole two years, the only non-target damage recorded was a single pustule of spores of *P. carduorum* on one out of 32 globe artichoke plants tested (Baudoin et al. 1993). It is this single pustule that has led to the inclusion of this case study here. This incident was 'predicted' by glasshouse tests and did not occur in a natural ecosystem.

It was concluded that "*P. carduorum* poses no threat to the non-target species tested" (Baudoin et al. 1993) and the rust was allowed to spread from the trial site in Virginia. The agent established in the USA and it has not been found on any non-target species in the field since release (W. L. Bruckart, personal communication).

Note that initially *P. carduorum* was only wanted for musk thistle control on the eastern side of the USA. It was proposed more recently that it should also be used in the west, specifically in California (Bruckart 2005). Authorities consequently requested further testing of seven rare-and-endangered native North American *Cirsium* species and four modern artichoke lines that grow in the Western USA (Bruckart 2005) and this data has been added to Table 1. Minor disease symptoms developed on some of the artichoke cultivars in the glasshouse but not on the native thistles. The rust could not be maintained on artichoke, even under optimal glasshouse conditions, and so these results confirmed earlier findings. Meanwhile, the rust has been naturally moving westwards in the USA, and it has in fact been found in California (Bruckart 2005). The permit request has been pursued despite this so that people can legally move the rust to where it is needed (Bruckart 2005).

2. Biological control of *Parthenium hysterophorus* (Parthenium weed or false ragweed) with *Puccinia melampodii* (rust)

Parthenium (Asteraceae) originated in the Neotropics and has become a problem in rangelands, especially in tropical areas in northern Australia (Queensland) and India (Evans et al. 2001). It competes aggressively with more desirable vegetation, but more importantly, it causes allergic responses, respiratory problems, and dermatitis in susceptible people.

The rust *Puccinia melampodii* was identified as a potential agent and was applied to 63 non-target species of relevance to Australia in the glasshouse. Symptoms developed on six non-target Asteraceous species: three weedy daisies, a variety of *Zinnia elegans*, sunflower (*Helianthus annuus*), and two varieties of marigold (*Calendula officinalis*) that are commonly available in garden centres in Australia (and the UK). Authorities decided to release the rust in Australia because the benefits were perceived to outweigh the potential costs.

However, prior to decision regarding release of the pathogen in India, further tests (outdoors, in Australia) were performed on marigold and sunflower cultivars grown commercially there. In those outdoor tests, two Indian cultivars of *C. officinalis* (different cultivars to those tested previously) were found to be quite susceptible to the rust. This is the incident of 'non-target attack outdoors' that has led to the inclusion of this case study.

As a result of these outdoor test results in Australia, the Project Directorate of Biological Control (the organisation seeking biocontrol agents for India) and CABI (the organisation that performed the host range tests) decided not to apply to the Indian government for permission to release *P. melampodii* in India (Marion Seier and Carol Ellison, personal communication; see also Barton (née Fröhlich) 2004). *Puccinia melampodii* was released in Australia in 1999. It has not been reported from any other non-target plants since release (L. Morin, personal communication).

3. Biological control of *Acacia saligna* (Port Jackson willow) with *Uromycladium tepperianum* (gall-forming rust)

Acacia saligna is a small tree from Western Australia that became a major weed in parts of South Africa. It often forms dense stands at the expense of native vegetation and is difficult to clear since it coppices after cutting and regenerates *en masse* from a large soil-stored seed-bank after fires (Richardson and Kluge 2008). One of the worst impacts of the weed is that it can totally replace areas of natural fynbos (Morris 1991) a geographically limited and particularly species-rich vegetation-type.

The rust *Uromycladium tepperianum* attacks *A. saligna* in its native range in Australia and was proposed as a potential biological control agent. It causes galling on stems, branches, phyllodes and reproductive organs and the formation of witches brooms on branches (Morris 1987). Severely affected trees seem more susceptible to drought and other stresses and have higher annual rates of mortality than uninfected trees (Morris 1997).

The rust has been recorded from a number of *Acacia* species in Australia, but testing revealed that particular isolates of the rust were specific to particular *Acacia* species (Morris 1987). Spores from galls on *A. saligna* were applied to 23 species of *Acacia* and *Albizia* and *Faodherbia albida* (Delile) A. Chev. (=*Acacia albida* Delile) that had been selected by a botanist as representative of the various groups of African acacias. In addition, the rust was applied to 22 *Acacia* species and a species from a closely related genus (*Paraserianthes lophantha* (Willd.) I. C. Nielson) that are native to Australia (=47 non-target species in total) (Morris 1987). Note that these figures (and those in the paragraph below) differ from those provided previously (Barton (née Fröhlich) 2004) due to errors in interpretation made by this author.

In these tests minor symptoms (e.g. necrotic or chlorotic spots) developed on 11 of the Australian species, and seedlings of three of the African species (but not two-year-old plants of these three species), but no galls or spores were formed and this was perceived to be a "resistance reaction" (Morris 1987). On six species (all from Australia) there was some gall development. However, the galls did not produce spores, grew slowly and remained small and were often partially necrotic (Morris 1987). These six species were: *Acacia myrtifolia* (Smith) Willd., *A. cyclops* Cunn. ex Don, *A. rigens* Cunn. ex Don, *A. terminalis* (Salisb.) J. F. Macbr., *A. pulchella* R.Br. and *Paraserianthes lophantha* (Morris 1987).

The researcher who conducted the host range tests pointed out that symptoms observed on these five species in glasshouse-grown seedlings may not indicate that they would be "natural hosts" of the *U. tepperianum* isolate from *A. saligna* in the field. He noted that "galls were never observed on *A. pulchella* and only one small gall was found on *A. cyclops* in south western Australia where the two species grow in mixed communities with heavily galled *A. saligna* (M. J. Morris, pers. obs. in Morris (1987)). It was concluded that the only potential 'cost' of releasing the *U. tepperianum* isolate from *A. saligna* would be minor damage to a few species of Australian *Acacia*, and *P. lophantha*. This was easily outweighed by potential benefits from a reduction in *A. saligna* populations, so the rust was released in South Africa in 1987.

Since its release *U. tepperianum* has occasionally caused abnormal galls on *Acacia cyclops* and *Paraserianthes lophantha*, as it did in pre-release testing (M. J. Morris, A. Wood, and J. Hoffmann, personal communication). As predicted, this only occurs in South Africa, as in Australia, where the non-target plants grow in close proximity to heavily infected *A. saligna* plants. As in the glasshouse, these galls are small, slow-to-develop and do not produce spores (A. Wood, personal communication). Thus, this non-target attack was correctly predicted.

4. Biological control of *Rubus fruticosus* agg. (Blackberry) with *Phragmidium violaceum* (rust)

Blackberry is the common name given to a cluster of closely related *Rubus* species called *Rubus fruticosus* agg. for convenience. It is from Europe and has become a serious weed in many countries, including Australia and New Zealand (Bruzzese and Lane 1996). It grows and spreads vigorously because seed is spread by fruit eating birds and mammals and it can also propagate vegetatively from cane tips. Stems are densely covered with spines (prickles) which are problematic for grazing animals and humans.

Phragmidium violaceum was chosen as a promising agent and a mixture of 15 isolates of the rust was applied to 51 non-target species all in the Rosaceae family. It caused symptoms on 15 *Rubus* species and for several species more than one variety was found to be susceptible. Note that nine of these 15 species were targets: i.e. *Rubus* species that had naturalised in Australia and were considered unwanted, noxious weeds (the author missed that fact and erroneously stated 15 non-target species had been infected in Barton (née Fröhlich) 2004). The remaining six species were 'non-targets'. These were: *R. rusticanus* Merc. (potentially used in breeding commercial varieties of blackberry), several unnamed varieties of 'brambleberry', *R. gunnianus* Hook. (native to Australia, specifically to Tasmania) and three *Rubus* species that are native to New Zealand: *Rubus*

australis Forst., *R. cissoides* A. Cunn., and, *R. schmidelioides* Fritsch (Bruzzese and Hasan 1986a). Seven other *Rubus* species native to Australia and two native to New Zealand were included in these tests, but were found to be immune or resistant to the rust (Bruzzese and Hasan 1986a).

The *Rubus* species native to Australia and New Zealand that developed symptoms in the original tests underwent further glasshouse testing in order to quantify the degree of attack by the rust (Bruzzese and Hasan 1986b). Note that these are the seven species recorded as having been tested twice in columns 5 and 6 of Table 1. It was concluded that "damage to *R. gunnianus* is likely if the 15 rust isolates tested were introduced to Australia for biological control of European blackberry. Damage to *R. schmidelioides* and *R. cissoides* can be expected if the rust reaches New Zealand, but the rust is unlikely to affect adversely the other Australian and New Zealand species tested" (Bruzzese and Hasan 1986b).

Subsequently, it was decided that the rust should be released in Australia because potential benefits were seen to outweigh potential costs. Blackberry itself was perceived to be a potential threat to native *Rubus* species, so a decision not to introduce the rust could also have had negative impacts on them. Note that the susceptible *Rubus* species native to Australia and New Zealand were described as "not economic plants, nor are they listed as endangered species" (Bruzzese and Hasan 1986a). In the 25 years since those words were written attitudes towards native species have altered dramatically in Australia and New Zealand and significant damage to such species would be far less tolerated today (personal observation).

Phragmidium violaceum appeared in Australia in 1984, and it is assumed that one or more illegal introductions were made before permission to release was granted (Evans et al. 2000). The rust first appeared in New Zealand in 1990 and subsequent DNA analysis suggests that *P. violaceum* in New Zealand originated from Australia, probably via wind-dispersal of urediniospores across the Tasman Sea (Gomez et al. 2006). One isolate of the rust (F15) was deliberately (and legally) released in Australia in 1991 and 1992 but DNA analyses suggest that genes from this strain were not widely incorporated into the existing population of the rust in Australia (Evans et al. 2000).

Between 2000 and 2009 surveys were conducted in New Zealand to specifically look for non-target damage from five pathogens that attack weeds there, including *P. violaceum* (Waipara et al. 2009). During that survey, the author found *P. violaceum* on two out of 132 *Rubus cissoides* plants examined. The rust was not found on any of the 69 plants of *R. schmidelioides* that were examined during the same study, despite this species having been found to be almost as susceptible in pre-release tests (Bruzzese and Hasan 1986b). The predicted damage observed in the field on *R. cissoides* was minor and occurred where this plant was growing beside heavily infected plants of the target weed.

Since it first appeared in Australia *Phragmidium violaceum* has proved useful for the control of some weedy *Rubus* taxa in Australia, but not others (Evans et al. 2005). It was proposed that more isolates of the rust should be sourced from Europe in order to broaden the genetic diversity of the rust population there (Gomez et al. 2008). In order to collect a broad a range of *P. violaceum* isolates that were likely to be effective against the particular *Rubus* taxa that are problematic in Australia a 'trap garden' was established. This method involved planting various clones of blackberry collected in Australia, each with a different DNA phenotype, at the CSIRO European Laboratory near Montpellier, France where *P. violaceum* occurs naturally (Morin et al. 2011). This method proved efficient: eight genetically distinct isolates of *P. violaceum* were obtained from the 'trap' plants and these were imported into Australia for host range testing (Morin et al. 2011). The non-target plants included in these tests were: (1) six commercial blackberry cultivars with *R. fruticosus* agg. in their pedigrees; and, (2) five *Rubus* species native to Australia (two tested previously and three described since the original tests were done, L. Morin and K. J. Evans unpublished data). Two non-target plants developed disease symptoms: the American thornfree cultivar of blackberry (which was also susceptible in earlier tests) and the native species *R. moorei* (which was 'resistant' to the old isolates) (L. Morin and K. J. Evans unpublished data). It was concluded that the new isolates had a similar cost:benefit ratio to the old ones, and they were released in Australia in 2004. *Rubus cissoides* plants were searched for *P. violaceum* at two sites in New Zealand in 2008–2009 and they were found to be free of the rust (Waipara et al. 2009).

Also, land managers in New Zealand have been asked to report to the author if they ever encounter *P. violaceum* on native *Rubus* species (Barton et al. 2008), and to date, no-one has done so. Therefore, if new genetic material has reached New Zealand from Australia it has not yet resulted in significant damage to non-target plants here.

Note that *Phragmidium violaceum* was discovered in April 2005 on Himalaya Blackberry (*Rubus armeniacus*) in Oregon, USA (Osterbauer et al. 2005). This appears to be an accidental introduction and is the first official report of the rust in North America. In Oregon, *P. violaceum* has so far been found on invasive *Rubus* species and one commercially farmed "Everthornless" Thornless Evergreen Blackberry (*Rubus laciniatus*) (Osterbauer et al. 2005). These species were susceptible in host range testing (Bruzzese and Hasan 1986a). The rust has not been found on *Rubus* species native to the US or other cultivated varieties. Therefore, while the rust is of concern to American horticulturalists who cultivate *R. laciniatus* varieties, its arrival is probably welcomed by land managers who seek to control blackberry. Note that DNA analysis conducted in Australia has shown that the rust that appeared in Oregon did not originate there (L. Morin, personal communication).

5. Biological control of *Mikania micrantha* (Mikania or mile-a-minute weed) with *Puccinia spegazzinii* (Rust)

Mikania is a vigorous, perennial vine that is native to the neotropics between Mexico and Argentina (Ellison et al. 2008). It has become an important invasive weed in many parts of Asia that have a moist, tropical climate (Ellison et al. 2008). It is known as mile-a-minute weed because it grows extremely fast and it is destructive because it can quickly dominate ecosystems and smother more desirable plants.

Puccinia spegazzinii was selected as a promising biological control candidate (Ellison et al. 2004). This rust occurs on *M. micrantha* throughout the native range of the plant (Ellison et al. 2008). Cross inoculation studies showed that most (possibly even all) of the exotic and weedy populations of *M. micrantha* are susceptible to one or more isolates of *Puccinia spegazzinii* (Ellison et al. 2004). An isolate of *P. spegazzinii* collected in Trinidad and Tobago was selected for initial host range testing by CABI in the UK. It was applied to 59 non-target species, of which 33 were from the same family as the target weed (the Asteraceae) (Ellison et al. 2008). The rust infected and developed spores on four of the non-target plant species: *Mikania capensis* DC., *M. cordata* (Burm. F.) Robinson, *M. microptera* DC., and *M. natalensis* DC. (Ellison et al. 2008). Of these, *Mikania cordata* supported the most vigorous rust development (Ellison et al. 2008).

This project is unusual in that the weed is so widespread that the biological control agent was wanted by five different regions: China (mainland), Taiwan, Fiji, India and Papua New Guinea (PNG) (Ellison and Day 2010). Each region conducted its own host range tests in addition to those performed in the UK. Test results were consistent: that is spores were not produced on any plants in this second round of testing that were not also shown to be susceptible in the UK tests.

The species of *Mikania* found to be susceptible to *P. spegazzinii* in host range tests are native to Africa (*M. capensis*, *M. microptera* and *M. natalensis*) and to Southeast Asia (*M. cordata*). There are no native *Mikania* species found in India, so risk assessment there was simple and the rust was released in Assam (NE India) in 2005 and in the Western Ghats in Kerala (SW India) in 2006 (Ellison and Day 2010). Apparently the rust failed to establish in both regions and the project is not presently active in India (Ellison and Day 2010).

Mikania cordata occurs naturally in China, PNG, Solomon Islands and Western Samoa, and so it was known that *P. spegazzinii* would overlap in range with this susceptible non-target plant in its native range if it were released in China and the Pacific. Therefore, there was a potential 'cost' to releasing the rust there. In weighing up this cost, it was taken into account that: (1) glasshouse tests are a worse-case scenario and disease symptoms that develop in the field are likely to be less severe (this issue is discussed further below); (2) if *P. spegazzinii* were to attack *M. cordata* in the field, it is unlikely to cause the species to become extinct (evolution does not favour biotrophic pathogens that eradicate their hosts); (3) the niche occupied by *M. cordata* includes altitudes where *M. micrantha* and *P. spegazzinii* do not thrive and these habitats should support populations of *M. cordata* that can evade and/or survive the

rust; and (4) *M. micrantha* is invading and destroying habitats where *M. cordata* occurs, so not releasing *P. spegazzinii* as a biological control agent for *M. micrantha* would also result in a 'cost' to *M. cordata* (Ellison et al. 2008).

Puccinia spegazzinii was subsequently released in China, Taiwan, Fiji and PNG (see Table 1 for dates). On the Chinese mainland it initially spread from release sites, but its current status in the field is not known (Ellison and Day 2010). It has reportedly established in Taiwan, Fiji and PNG (Ellison and Day 2010).

In December 2010 *Puccinia spegazzinii* was found infecting the native species *Mikania cordata* in the field in PNG (Ellison and Day 2010). Rust pustules were found on the leaves of a small population of *M. cordata* at a single site (Kiteni Kurika, personal communication). At this site infected vines of the two *Mikania* species (target and non-target) grow "on top of each other" (Kiteni Kurika, personal communication). Infection was quite heavy on both plant species, but on a return visit, there were found to be fewer plants of the target weed while the native species was still present in large numbers (despite still being highly infected). It seems that *M. cordata* is most likely to be infected by the rust when it grows in close proximity to infected *M. micrantha*. If the rust successfully reduces populations of *M. micrantha*, as appears to be happening in the field already, then hopefully, there will be fewer areas where such 'spill-over' can occur in future. Researchers in PNG are continually checking whether the rust is attacking *M. cordata* in other areas, especially at the small number of places where target and non-target plants grow together (M. Day, personal communication). This non-target attack was accurately predicted, and so far it seems that the expectation that *M. cordata* that grows in habitats that are unsuitable for *M. micrantha* will be able to evade and survive the rust is being realised.

Expansion of host range under artificial conditions

Pathogens released for the biological control of weeds have apparently only ever caused damage to six non-target species outdoors, yet those same agents damaged 107 non-target species in pre-release tests conducted indoors (Table 1). Thus, host range tests under glasshouse conditions have tended to over-estimate the susceptibility of non-target plants in the field.

There are two reasons for this: firstly, host range tests are invariably conducted under conditions believed to be 'optimal' for the pathogen. That is, before host range tests begin experiments are performed to determine: the temperature range at which the pathogen is most active, and whether or not it requires free-moisture to infect its host, and if so, how long this 'dew period' should be (see, as a typical example, Ellison et al. (2008)). Host range tests are then conducted within an environment heavily skewed in the pathogen's favour so as to ensure that positive control plants (i.e. the target weed) become heavily diseased. These ideal conditions are likely to be rare in the field and so test results in containment present a 'worse-case-scenario'. The second reason why indoor tests tend to over-estimate outdoor damage is that plants used in tests have often been grown from seed in a glasshouse. As a result they can have softer, less pathogen-resistant tissues than cohorts, which have grown through and survived various hardships, outdoors (Barton (née Fröhlich) 2004).

Additional information useful for risk assessment

When weighing up the costs and benefits of a potential release, authorities should look at other information in addition to the results of host range tests done under artificial conditions. Otherwise, pathogens that could be useful (and safe) biological control agents for weeds could be prematurely rejected.

Examples of additional information being provided to assist decision makers are plentiful in the biological control literature, including in the case studies discussed above. For example, information on the field host range of a pathogen in its new home can be gathered through observation of its behaviour in its old one. It was known that the rust *Uromycladium tepperianum* would probably form non-sporulating galls on some Australian *Acacia* species in South Africa, because that is what it does in Australia (Morris 1987). Likewise, it was thought that *Puccinia carduorum* would probably not cause significant damage to globe artichoke in the field in the USA,

because it does not attack that species in the field in its home range in Eurasia (Bruckart et al. 1985).

Another way for researchers to assist decision makers is to quantify the susceptibility of the non-target plant(s) with respect to the target plant. This can be done on the basis of disease severity (e.g. disease ratings, leaf area infected, reduction in plant height or weight) or disease incidence (i.e. the proportion of individual non-target plants infected compared to the target plants). A good example of this technique is provided by the second set of tests conducted on blackberry rust (*Phragmidium violaceum*) in order to compare the susceptibility of various desirable and undesirable *Rubus* species (Bruzzese and Hasan 1986b).

Finally, the ideal situation, which is often impossible in practice, is for host testing to be done outdoors. Probably the best way of doing this is to export test plants to somewhere where the pathogen has already been released (as was done with Indian plants being tested in Australia as part of the *Parthenium* project, see above). Tests outdoors could also be done in the home-range of the pathogen. The main obstacle to such tests is getting permission to grow plants from one country outdoors in another, outside of a quarantine facility. Note that this is sometimes possible: for example it was done in France with 'trap gardens' of Australian *Rubus* species (see above). The situation which is likely to give the best prediction of post-release behaviour is unfortunately the one with greatest risk: that is setting up plots of non-target plants outdoors in the country where the agent is to be used (as was done with thistle rust, *Puccinia carduorum*, in the USA). This is the ideal experiment in that the organism is being tested under exactly the conditions it will encounter after release. However, it is a brave researcher who undertakes to eradicate a pathogen, especially one as mobile as a rust, once it has been 'let out of the bottle'.

Conclusions: predictability of pathogen host range and its relevance to the use of pathogens for classical biological control in natural areas

It was 1971 when the first pathogen was deliberately released as a classical biological control agent against a weed (Hasan 1972). Since then, there has not been a single reported case of unpredicted non-target damage. While pathologists working in this field deserve a pat-on-the-back for that, there is no room for complacency. It is a very serious responsibility to ensure that the results of biological control projects reduce, and not add-to, the adverse impacts of exotic organisms in natural areas.

Researchers recognise this, and in the author's experience, they are always looking for data that will improve the accuracy of their predictions with respect to non-target attack in the field. Directed surveys for non-target damage from pathogens released as classical biological control agents are rare, and published information even rarer (personal observation). This is unfortunate as information about non-target impacts in the field would help refine host-range testing methods and potentially reduce 'false positives'. There are many obstacles to conducting long-term post-release monitoring studies (Barton (née Fröhlich) 2004; Hopper 2001) but it is possible. Retrospective studies of non-target damage by both pathogens (Waipara et al. 2009) and invertebrates (Paynter et al. 2004) have been done in New Zealand. Also, many such studies have been done with specific insects introduced to control weeds, especially in the US (see, for example, papers cited in Louda et al. (2003) and listed on p. 43 of Hopper (2001)).

Once the fundamental host range of each potential agent has been determined (through host range testing of appropriate non-target species indoors) other information must be added in order to gain a picture of how it is likely to behave in the field. Examples of 'other' information include: the taxonomy, life-cycle and epidemiology of the agent; the presence/absence of 'susceptible' non-target plants where the agent will be used, and the vulnerability of those plants; and the ecology and behaviour of the agent in its native range. The results presented here show that when all this information is put together, pathogen host range in the field can be predicted accurately.

In 2004, pathogens had only been released as classical biological control agents for weeds in seven countries: Argentina, Australia, Chile, French Polynesia, New Zealand, South Africa and the USA (including Hawaii) (Table 1). At that time, the author said "Given their excellent safety record, it is to be hoped that more countries will be added to this short list in the future" (Barton (née Fröhlich) 2004). It was therefore very pleasing to find that as a result of the

project to control Mile-a-minute-weed (*Mikania micrantha*) pathogens have since been released in four more countries (China (mainland and Taiwan), Fiji, India and Papua New Guinea, Table 1). It is to be hoped that more countries will follow in due course.

The predictions of pathogen host range in the field that have been made to date have led to appropriate decisions: the environmental costs of releasing them have never outweighed the environmental benefits. Pathogens should be seen as a particularly useful tool for weed control in natural areas which are rich in valued non-target species.

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