Ecological, practical, and political inputs into selection of weed targets: What makes a good biological control target?

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Abstract

The topic of ecological, practical, and political considerations in the selection of weed targets for biological control has been widely discussed during the past two decades, mostly from the perspective of insect herbivores. For conceptual and practical purposes, plant pathogens have been treated in these discussions as if they are a subset of inoculative biocontrol agents, with little said about the inherent differences between pathogens and insects as biocontrol agents or the selection of weed targets for control by the inundative, bioherbicide strategy. Herein, I attempt to address the question of what makes a good biological control target for plant pathogens used as inoculative as well as inundative agents, basing my analysis on examples from the past three decades. Despite the small number of examples available for this analysis, the following generalizations can be made: (1) Weeds with robust capacity for vegetative regeneration are more difficult to control with pathogens than those that lack this trait. (2) A plant’s growth habit is not a reliable guide for target selection; weeds that have been successfully controlled include annual and biennial herbs, perennial shrubs, perennial vines, and trees, while numerous failures have been reported irrespective of the target’s growth habit or reproductive mode. (3) It is more challenging to control species with genetic heterogeneity and capacity for introgression than genetically homogeneous and reproducitively conserved species. (4) Matching the target host’s susceptibility with the candidate pathogen’s virulence is of utmost importance for biocontrol success since host–pathogen interactions at the species and subspecies levels are often governed by single-gene differences (e.g., varietal specificity). (5) Practical and political considerations are central to the selection of targets for control with pathogens. (6) Demand from influential stakeholders for control and/or for a nonchemical or economically sustainable control typically drives the initiative as well as the continuance of biocontrol projects to their completion. (7) In the case of inundative, bioherbicide agents, the continuity and ultimate implementation of a project will be dictated by the prospects of economic returns from developing and using a pathogen. (8) The stakeholders’ perceptions of the effectiveness of a biocontrol program can be unpredictable, leading to conflicting views of “success.” In the final analysis, a good weed target for control by a pathogen is one that has strong stakeholder backing and the list of available pathogens for the target suggests a possibility of acceptable control at a cost that is competitive with those of other control options. While this conclusion is also applicable to target selection for insect biocontrol agents, it is more relevant for pathogens because of limited funding and personnel available for development of pathogens and the added cost and technological complexity of implementing bioherbicides compared to classical biocontrols.

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Keywords: Weed biocontrol; Target selection; Plant pathogens; Classical biological control; Bioherbicides; Selection criteria

1. Introduction

In the past two decades, several authors have attempted to explain what makes a good weed target-agent combination in biological control by relating the target’s attributes, such as growth habit, reproductive mode, and others, with biocontrol success. The expressed or implied aim has been to devise ways to pick the right agents and targets. The majority of these discussions have been from an entomological perspective, and it is worthwhile to review some key concepts that
have been presented. For example, Burdon and Marshall (1981) proposed that the weed’s reproductive mode, whether it is asexual or sexual, relates to success in biocontrol; they claimed that asexual species historically have been effectively controlled more often than sexual species, although 10 years later the data no longer seemed to support this view (Chaboudez and Sheppard, 1995). Crawley (1989a) argued that certain plant attributes are associated with good control, notably genetic uniformity in weed populations, lack of perennation or dormancy, and susceptibility to secondary infection. Crawley (1989a) also noted that plants with rhizomatous, perennial growth-form and high capacity for regrowth as well as those that constitute low food quality for insects are poor targets. A reexamination of the relationships of weeds’ reproductive mode and life history attributes to biological control success by Chaboudez and Sheppard (1995) did not support these earlier views. Straw and Sheppard (1995) found that biocontrol projects have been more successful against herbs than against shrubs and trees. However, Cullen (1995) has argued that it is rather futile to predict the effectiveness of biological control based on one or more of the weeds’ attributes, and the post-release success rate for insects released for classical biological control is, at best, only 35% (Crawley, 1989b; Ehler and Hall, 1982; McFadyen, 1998; Williamson and Fitter, 1996). Sheppard (1992) has concluded that the success rate is much higher, possibly around 65%, if the analyses were based on weed targeted rather than on agents released. Fowler (2000) has aptly pointed out that success rates for weed biocontrol projects are in the range 50–80% when adequate funding and suitable commitments have been made; inadequate and inconsistent support is often the leading cause of unsatisfactory control. Nonetheless, several serious attempts have been made to prioritize biological control projects to justify allocation of research resources as well as to improve the odds of successful outcome (Palmer and Miller, 1996). Rating systems have even been designed to select the best biocontrol targets (Peschken and McClay, 1995), and potential agents (Sheppard, 2003). Target selection however is not always by unanimous choice since conflicting interests frequently play a part in the selection process. Conflicts of interest facing biological control programs, which have nothing to do with the ultimate success or failure of a biological control program, have the utmost potential to stop a program from being implemented. Thus, practical considerations such as stakeholders’ support for the program, perceptions of conflicting interests, and economic feasibility, play a significant role in the selection of weed targets for biocontrol (DeLoach et al., 1996; Freeman and Charudattan, 1985; Harris, 1985; Turner, 1985).

With the exception of a few of these cited references, the topic of target selection has not been viewed from the plant pathogen perspective. Pathogens are unlike insects in one key aspect: insect herbivores have evolved to use plants as a food source and a habitat for reproduction. Hence, in principle, they cannot kill their hosts without risking their own survival. Their success as biocontrol agents must therefore be measured by their non-lethal effects that impose an energy drain and thereby reduce host biomass, competitiveness, and population density. Plant pathogens, on the other hand, can have different levels of adaptation to their hosts: some have evolved towards balanced parasitism (i.e., biotrophs) and consequently do not kill their hosts outright. Even though biotrophic pathogens can kill cells, tissues, and even whole plants by eliciting a hypersensitive response, as part of their life-history strategy, they sustain their life cycles without eliminating their source of sustenance. In this respect, biotrophic pathogens are comparable to insect herbivores; they bring about biological control by imposing a chronic energy drain on their hosts. The vast majority of pathogens however are necrotrophs that must kill their hosts or host tissues to derive nourishment; this ability to kill their hosts outright makes these pathogens highly suitable agents for weed biocontrol.

Given the wide latitude in the capacity of pathogens either to kill or not kill their hosts, the question of what makes a good target for biological control by pathogens should be examined primarily from the perspective of the pathogen’s destructive capability. Important in this regard are the pathogen’s capacity to inflict damage (pathogenicity), the intensity of that damage (virulence or aggressiveness), and the environmental amplitude under which the disease can occur (whether a pathogen is capable of causing disease under a wide or narrow range of environmental conditions prevalent in the target weed’s geographic range).

With limited resources available for research on plant pathogens compared to insect biocontrol agents, or chemical herbicides, the selection of targets for control by pathogens has followed a very pragmatic course, choosing targets that can garner adequate support. Herein, I will attempt to analyze the record of biological control of weeds by using plant pathogens to answer the question, “what makes a good weed target for biological control with plant pathogens?”

2. Materials and methods

This is a retrospective analysis. The projects examined for this analysis were compiled for a previously published review (Charudattan, 2001a) which was supplemented with information in Julien and Griffiths (1998) and the author’s assessment of unpublished accounts (e.g., International Bioherbicide Group meeting abstracts; International Bioherbicide Group, 2005).
The list of projects was updated with reports presented at the Eleventh International Symposium on Biological Control of Weeds held in 2003 in Canberra, Australia (Cullen et al., 2004).

The success rates of the projects examined are given in Table 1. The projects were categorized as verifiable success, partial success, and uncertain for inoculative agents and verifiable success, uncertain, and untried/ineffective for inundative agents, using different standards for inoculative and inundative agents. For inoculative agents, verifiable success meant an acceptable level of control in at least one country or a large region (e.g., county, state, or province). For inundative agents, the agent’s registration or approval as a bioherbicide and its use with some regularity constituted verifiable success. Publications in refereed journals and a general recognition that a project has yielded positive results acceptable to stakeholders formed the basis for this categorization. The category verifiable success was created as a way to answer divergent views of what constitutes “success.”

Partial success was assigned when development and deployment of an inoculative agent was complete but its impacts are not clear or still evolving. Uncertain inoculative agents are those that could be developed and deployed, but the prospects of this happening are uncertain. Also included here are agents that have been deployed but are having little impact on their weed targets.

When an inundative agent has been developed and registered as a bioherbicide, the research and development efforts reach a significant milestone. Yet, the real success of the project would not be realized unless the bioherbicide product is used with some regularity. Hence, its use and impacts remain uncertain. Untried/ineffective agents are those that have not progressed beyond initial exploratory evaluations, typically in academic settings.

I expect some of the partially successful projects involving inoculative agents to progress to the verifiable success category in the coming years as the impacts of the pathogens become more pronounced. Likewise, some of the projects in the uncertain (inoculative and inundative) category may move up to the partial success or verifiable success category if additional efforts are made to augment the inoculative agents or use the bioherbicide products. It is also possible that, with time, an improved historical perspective will justify downgrading of some projects from successful to less successful categories. Published and unpublished accounts were reviewed to verify assignment of projects to these three categories. In some instances, the principal scientists involved were queried.

Several examples of accidental or natural (unintentional) introductions of pathogens that have resulted in noticeable levels of weed control (see Julien and Griffiths, 1998), were examined but unless a specific program was mounted to document the impacts or to further augment the agents, these examples were not included in this analysis. When a pathogen had been used against the same weed in more than one country, it was counted as one project. When the same weed was targeted for control by different pathogens, the projects were counted separately. Two broad host-range pathogens (Chondrostereum purpureum and Sclerotinia sclerotiorum) have been developed for use against more than one weed target; each of these is considered a single project.

The growth habit (herb, shrub, tree, etc.) and the reproductive mode (reproduction by seed or clonal) of the targets were examined for their association with success. Information on the genetic makeup and potential for introgression is not readily available for all targets; so the best available information was used in the analysis. Practical and political considerations, such as stakeholder demand for control, and economic feasibility for development and use of a pathogen (i.e., marketability) also were considered, drawing from personal experience.

A caveat: these examples of weed control with plant pathogens represent a very small sample size, even smaller than the number of projects with insects during the same period of three decades, 1970–1999. This small number of examples is not amenable to statistical analysis. Moreover, assigning projects as “verifiable,” “partial,” or “uncertain” regarding success is admittedly somewhat arbitrary. Hence, caution is urged in interpreting the following analyses and conclusions.

<table>
<thead>
<tr>
<th>BC strategy</th>
<th>Verifiable success</th>
<th>Partial success</th>
<th>Uncertain</th>
<th>Untried/ineffective</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inoculative (classical)</td>
<td>6 (28.6%; 7.2%)⁷</td>
<td>6 (28.6%; 7.2%)</td>
<td>9 (42.8%; 10.8%)</td>
<td>Not applicable</td>
<td>21</td>
</tr>
<tr>
<td>Inundative (bioherbicide)</td>
<td>5 (8.1%; 6%)</td>
<td>Not applicable</td>
<td>12 (19.4%; 14.5%)</td>
<td>45 (72.5%; 54.2%)</td>
<td>62</td>
</tr>
<tr>
<td>Total</td>
<td>11 (13.3%)⁷</td>
<td>6 (7.2%)</td>
<td>21 (25.3%)</td>
<td>45 (54.2%)</td>
<td>83</td>
</tr>
</tbody>
</table>

⁷ Based on Charudattan (2001a). N = 83 weed–pathogen projects. See Section 2 for description of how the categories were devised.

Table 1
Success rates of projects using plant pathogens as biological control agents of weeds

A. Based on Charudattan (2001a). N = 83 weed–pathogen projects. See Section 2 for description of how the categories were devised.

B. The first percentage refers to proportion within the biological control strategy category (in-row percentage); the second percentage refers to proportion out of all pathogen projects (i.e., 83).

C. Percentage of all projects (i.e., within this row).
3. Results and discussion

3.1. Growth habit

Weed targets of the six verifiably successful inoculative biocontrol programs included a tree species, two perennial shrubs, a perennial herb, and two perennial vines (Table 2). Targets in the partially successful inoculative biocontrol projects included one herbaceous perennial creeper, two perennial shrubs or small trees, a biennial herb, an annual or biennial herb, and a perennial shrub. Targets in the uncertain group included a perennial shrub or small tree, one perennial shrub, three annual herbs, two perennial herbs, a perennial vine or shrub, and a perennial herb or shrub.

In the case of successful inundative biological control projects (verifiable success), the targets included one annual herb, broad-leaved trees (two projects; several target species), a perennial vine, and an annual grass. The uncertain group included broad-leaved trees (two projects), a perennial herb or shrub, a perennial herb, two perennial shrubs, two parasitic plants (Cuscuta spp.), an annual sedge, and three annual herbs. No associations can be identified in untried/ineffective projects as well. The only commonality in these failed projects is the “lack of efficacy,” of the pathogen candidates compared against a benchmark set by a chemical herbicide (reviewed in Charudattan, 1991, 2001a, with supplemental information from Barton, 2004; International Bioherbicide Group, 2005; Julien and Griffiths, 1998; Trujillo, 2005).

3.2. Reproductive mode

Among the successful inoculative projects (verifiable plus partial success), four targets reproduce by seeds and vegetatively, while eight by seeds only. Six of the targets in the unsuccessful (uncertain) inoculative projects reproduce by seeds only compared to three that are clonal and produce seeds. As noted above, there is a similar lack of association in the reproductive mode versus success or uncertain outcome of inundative agents. Uncertain/ineffective inundative projects, likewise, do not reveal any trends in this respect. Thus, it is not possible to relate the targets’ reproductive mode to the success or failure of these programs.

3.3. Genetic heterogeneity and capacity for introgression

Weed targets with genetic heterogeneity and capacity for introgression may (Burdon and Marshall, 1981) or may not (Chaboudez and Sheppard, 1995) be more difficult to control than genetically homogenous and reproductively conserved species. Because many invasive weeds may pass through genetic bottlenecks during their introduction into adventive ranges, introduced exclusively asexual weeds are likely to give rise to genetically homogenous populations. The probability is high that such genetically homogenous populations will be attacked by locally adapted, virulent pathogens (Caesar, 1996, 2005). This is borne out by the examples in Table 1 in Charudattan (2001a) wherein 72% of the plants targeted for inundative control by indigenous pathogens are introduced weeds. Although introduced weeds are more often targets for biocontrol due to their adverse impacts on ecosystems, the availability of indigenous pathogens provides an impetus to develop them as bioherbicides.

Examples from the last three decades confirm that susceptibility of newly arrived weeds to indigenous pathogens is quite common; bioherbicide literature is replete with accounts of finding native pathogens with high levels of virulence that possibly can augment the effects of introduced biocontrol agents (e.g., Caesar, 1996; Charudattan et al., 1978; Klisiewicz, 1986; Mortensen, 1984; Woods and Fogle, 1998). Interactions between rust fungi, the most commonly used pathogens in classical biological control, and naturally occurring necrotrophic facultative parasites are also quite common (e.g., Hallett and Ayers, 1992; Morin et al., 1993). As Cook et al. (1996) have appropriately stated that “(a)griculture and forestry benefit greatly from the resident communities of microorganisms responsible for naturally occurring biological control of pest species, but additional benefits are achieved by introducing/applying them when or where needed.”

Yellow starthistle plants (Centaurea solstitialis L.) in central California were found to be susceptible to three naturally occurring fungal pathogens that appeared to play a role in regulating seedling recruitment (Woods and Fogle, 1998). At one study site in 1997–1998, 68% of the thistle seedlings that germinated in the fall died by the following spring. Yellow starthistle has also been reported to be susceptible to some fungal pathogens isolated from safflower (Carthamus tinctorius L.) and to three common plant viruses (alfalfa mosaic virus, lettuce mosaic virus, and turnip mosaic virus) (Klisiewicz, 1986). Yellow starthistle plants were occasionally killed by lettuce mosaic virus and turnip mosaic virus (Klisiewicz, 1986). Prior to this experimental evidence by Klisiewicz, turnip yellow mosaic virus was not known to infect yellow starthistle, much less kill it at the rosette stage (Plant Viruses Online, 2005). So, how common might be such deadly “new encounters,” waiting to be discovered and possibly exploited?

Natural incidences of root diseases have been shown to be a factor in the decline of leafy spurge (Euphorbia esula L.) stands in several areas of Montana, North Dakota, and Wyoming (Caesar, 1996). Strains of naturally occurring Fusarium oxysporum Schlect., F. solani (Mart.) Sacc., and F. proliferatum (T. Matsushima) Nirenberg predominated among the Fusarium strains.
<table>
<thead>
<tr>
<th>Weed</th>
<th>Pathogen</th>
<th>Growth habit</th>
<th>Predominant mode(s) of reproduction</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Verifiable success—inoculative agents</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ageratina riparia</em> (Spreng.)</td>
<td><em>Entyloma ageratinae</em> Barreto &amp; Evans</td>
<td>Perennial shrub</td>
<td>Seed, clonal</td>
<td>Barreto and Evans (1988); Morris (1991); Barton (2004); Trujillo (2005)</td>
</tr>
<tr>
<td><em>Chondrilla juncea</em> L.</td>
<td><em>Marasulia cryptostegiae</em> (Cummins) Y. Ono</td>
<td>Perennial vine</td>
<td>Seed, clonal</td>
<td>Evans (1993); Evans and Tomley (1996); Tomley et al. (2003)</td>
</tr>
<tr>
<td><strong>Partial success—inoculative agents</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Baccharis halimifolia</em> L.</td>
<td><em>Puccinia evadens</em> Harkn.</td>
<td>Perennial shrub, small tree</td>
<td>Seed</td>
<td>Verma et al. (1996); Tomley and Willsher (2002)</td>
</tr>
<tr>
<td><em>Centaurea solstitialis</em> L.</td>
<td><em>Puccinia jaceae</em> Otth.</td>
<td>Annual or biennial herb</td>
<td>Seed</td>
<td>Bruckart (1989); Shishkoff and Bruckart (1993); Suszkiw (2004)</td>
</tr>
<tr>
<td><em>Carduus pycnocephalus</em> L.</td>
<td><em>Mycosellus lantanae</em> (Chupp Deighton var. <em>lantanae</em>)</td>
<td>Perennial shrub</td>
<td>Asexual seed</td>
<td>den Breyen (2004); Trujillo (2005)</td>
</tr>
<tr>
<td><em>Clematis vitalba</em> L.</td>
<td><em>Phoma clematidina</em> (Thuem.) Boerema</td>
<td>Perennial vine, shrub</td>
<td>Seed, clonal</td>
<td>Seier and Evans (1996); Julien and Griffiths (1998)</td>
</tr>
<tr>
<td><em>Eichhornia crassipes</em> (Mart.) Solms-Laub.</td>
<td><em>Cercospora piaropi</em> Tharp. emend. Conway emend. Tessmann et al. (=<em>C. rodmanii</em> Conway)</td>
<td>Perennial vine, shrub</td>
<td>Seed, clonal</td>
<td>Gourlay et al. (2000); Charudattan et al. (1985); Charudattan (2001c)</td>
</tr>
<tr>
<td><em>Galega officinalis</em> L.</td>
<td><em>Uromyces galegae</em> (Opiz) Sacc. ex Fr.</td>
<td>Perennial herb, shrub</td>
<td>Seed</td>
<td>Morris (1991)</td>
</tr>
<tr>
<td><em>Heliotropium europaeum</em> L.</td>
<td><em>Uromyces heliotropii</em> Sred.</td>
<td>Annual herb</td>
<td>Seed</td>
<td>Barton (2004); Julien and Griffiths (1998)</td>
</tr>
<tr>
<td><em>Mimosa pigra</em></td>
<td><em>Diabole cubensis</em> (Arth.) Arth.</td>
<td>Perennial shrub, small tree</td>
<td>Seed</td>
<td>Seier and Evans (1996); Julien and Griffiths (1998)</td>
</tr>
</tbody>
</table>

(continued on next page)
<table>
<thead>
<tr>
<th>Weed</th>
<th>Pathogen</th>
<th>Growth habit</th>
<th>Predominant mode(s) of reproduction</th>
<th>Reference(s)¹ b</th>
</tr>
</thead>
</table>

### Verifiable success—inundative agents

**Aeschynomone virginica (L.) B.S.P.**

| Broad-leaved trees           | *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. in Penz. f.sp. aeshynome | Annual herb  | Seed                                | TeBeest and Templeton (1985) |
| *Poa annua* L.               | *Xanthomonas campestris* Migula pv. *Poae*                                              | Annual stoloniferous grass | Seed, clonal             | Imaizumi et al. (1997) |
| Senna surattensis (Burm. f.) Irwin & Barneby (=Cassia surattensis Burm. f.) | *Acremonium sp.*                                                                  | Tree          | Seed                                | Trujillo (2005) |

### Uncertain success—inundative agents

**Acacia spp.**

| Cylindrobasidium laeve (Pers.:Fr.) Charumis                     | Tree       | Seed, stump regrowth  | Morris et al. (1999) |
| Acroptilon repens (L.) DC.                                      | *Sabanguina picridis* (Kirj.) Brezeski                                              | Perennial herb, shrub | Seed, clonal           | Ou and Watson (1992, 1993) |
| Cirsium arvense and Ranunculus acris                           | *Sclerotinia sclerotiorum* (Lib.) de Baryd                                      | Perennial herb (both) | Seed, clonal (both)   | Hurrell et al. (2001); Bourdôt et al. (2004) |
| Clidemia hirta (L.) D. Don                                      | *C. gloeosporioides* f.sp. *clidemiae*                                             | Perennial shrub | Seed                                | Trujillo (2005) |
| Cuscuta campestris Yunecker and other spp.                     | *Alternaria cuscucataecidue* Rudak                                                | Annual or perennial parasite | Seed, clonal            | Templeton (1982) |
| Cypres cuscutaeus L.                                            | *P. canaliculata* (Schwein.) Legerh.                                               | Annual sedge          | Seed, clonal            | Phatak et al. (1983); Bruckart et al. (1988); Scheepens and Hoogerbrugge (1991) |
| Diospyros virginiana L.                                         | *Acremonium diospyri* (Crandall) W. Gams (=Cephalosporium diospyri Crandall)       | Broad-leaved tree     | Seed                                | Templeton (1982) |
| Malva pusilla Sm.                                               | *C. gloeosporioides*                                                               | Annual herb            | Seed                                | Mortensen and Makowski (1997) |
| Solanum elaeagnifolium Cav.                                    | *Nothunguina phylobia* Thorne                                                     | Annual herb            | Seed                                | Robinson et al. (1978) |

### Untried/ineffective projects—inundative agents

A total of 45 projects; data not included herein; see Charudattan (2001a)

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¹ Compiled from data in Charudattan (2001a); Julien and Griffiths (1998) and references cited herein. Seventy-nine weed–pathogen projects involving 70 weed species and 93 pathogen species and/or strains. See Section 2 for description of how the categories were devised.

² Only some key references are given here; for additional information and citations, see reviews by Charudattan (2001a); Barton (2004); and Trujillo (2005).

³ Asexual (apomictic) seed producers are identified as “asexual seed”; in all other cases listed, seed production is sexual.

⁴ Counted as one project, since the same agent will be used against two targets.
isolated from stunted and diseased feeder roots and crowns of leafy spurge plants sampled. *Fusarium* spp. were also the most frequently isolated fungi from leafy spurge plants having stem and root rots collected in the prairie provinces of Canada (Mortensen, 1984). Given the natural distribution of these fungi, the variety of species, levels of virulence, and compatibility groupings involved, as well their capacity to cause disease over a wide area, we cannot rule out the part played by native pathogens in the emerging picture of leafy spurge control.

A genetically heterogeneous plant population will tend to have a genetically diverse mixture of coevolved, host-adapted, pathotypes. Therefore, theoretically it should be possible to find a pathotype effective against all of the diverse weed forms. In the absence of such a pathotype, a biocontrol attempt based on a narrowly host-adapted pathotypes is likely to run into problems of resistant populations of the target. Our experience with *Phomopsis amaranthicola* Rosskopf, Charudattan, Shabana, and Benny (Rosskopf, 1997; Rosskopf et al., 2000, 2005) illustrates this point. Rosskopf determined that *P. amaranthicola* was host specific at the generic level, being pathogenic only to *Amaranthus* spp. but not to members in six other genera in the Amaranthaceae or to plants outside this family (Rosskopf, 1997; Rosskopf et al., 2005). All 21 *Amaranthus* spp. tested were susceptible and developed typical foliar and stem lesions, but the level of plant mortality from the disease was variable. In some species, different accessions registered levels of plant death ranging from 0 to 100% (Rosskopf, 1997). This situation is not surprising given the genetic heterogeneity and capacity for introgression in the genus *Amaranthus* (Franssen et al., 2001). Hypothetically, it is likely that some resistant species and genotypes may become more prevalent if *P. amaranthicola* were used widely and repeatedly as a bioherbicide for *Amaranthus* spp.

Bruckart et al. (2004) found differential susceptibility in Russian thistle (*Salsola tragus* L.) accessions from California to an isolate of *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. in Penz. collected in Hungary. Recent molecular analysis indicates that the California population of Russian thistle is composed of two cryptic, morphologically similar genotypes referred to as Type A and Type B. Type B is genetically different from Type A and may be a separate species from *S. tragus* (Ryan and Ayres, 2000). Although both types were susceptible to *C. gloeosporioides*, Type A sustained greater disease damage than Type B. While inoculation with the fungus resulted in a 60% reduction in the fresh weight of Type A compared to the uninoculated control, Type B sustained only 9% reduction. Hypothetically, if Type A were successfully controlled in California using *C. gloeosporioides*, populations of Type B may predominate over time, similar to the situation with the *Chondrilla juncea* L.–*Puccinia chondrillina* Bubak & Syd. system in Australia (Burdon et al., 1981; Espiau et al., 1998).

From the examples in Table 2, it was not possible to trace an association between the weeds’ genetic heterogeneity and capacity for hybridization and biocontrol success or failure. This is due to a lack of published information on the genetic composition of major weeds targeted for biological control. In the case of exotic invasive weeds, it is important to know the precise genetic make-up and population structure of the target weeds in the region where control will be applied; information about the genetic composition of the weed populations in their native range, while important, is immaterial without an understanding of the genotype(s) of the introduced metapopulation(s).

If we assumed that most, if not all, of the significant number of introduced exclusively asexual weeds have passed through genetic bottlenecks during arrival at their adventive regions, and that the correct pathogen types adapted to the target types were used in every case, then number of successes with classical biocontrol should be much higher than found in the literature for such species. However, experience from the *P. chondrillina–C. juncea* project indicates that genetic heterogeneity, even on a limited extent involving only three distinct clones, can detract from complete success of projects (see Section 3.5). If genotypic variability in such targets’ populations were commonplace, we would expect to see many more *P. chondrillina–C. juncea*-like cases, where biocontrol agents discriminate among the target genotypic clones and reveal the existence of genetic heterogeneity. Luckily, in the case of some important weeds like waterhyacinth (*Eichhornia crassipes* [Mart.] Solms-Laub.) or tropical soda apple, *Solanum viarum* Dunal, this does not appear to be the case.

### 3.4. Capacity for vegetative regeneration

Experience suggests that weeds with a robust capacity for regeneration following biotic attacks are more difficult to control than weeds with determinate growth habits. For example, one of the most challenging weed targets for biological control has been waterhyacinth (*E. crassipes*), a plant endowed with a strong capacity for vegetative regeneration. Pathogens considered to date for development as bioherbicides for this weed have all been foliar fungal pathogens that damage and reduce the foliar biomass without killing the entire plant (Charudattan, 2001b). Typically, waterhyacinth plants (ramets) sustain initial losses from disease, shed the diseased leaves through accelerated senescence, and, in the absence of continued disease pressure from rapid secondary disease cycles, compensate for the diseased leaves by producing healthy new growth (Charudattan et al., 1985). Consequently, the disease level and disease pressure are diluted and the plant regenerates and
repopulates. This type of host compensation for disease loss and the consequent dilution of disease impact are common in many weed–pathogen systems we have studied. Examples include hydrilla (*Hydrilla verticillata* L.f. Royle) and *Fusarium* spp. or *Mycotoxidiscus terrestris* (Gerdemann) Ostezeski; cogongrass (*Imperata cylindrica* L.) Beauv.) and *Bipolaris sacchari* (E.J. Butler) Shoemaker or *Dechslera gigantea* (Heald & F.A. Wolf) Ito; and purple nutsedge (*Cyperus rotundus* L.) and *Dactylaria higginsii* (Luttrell) M.B. Ellis. (R. Charudattan et al., unpublished). All three plants regenerate by vegetative growth from tubers, turions, rhizomes, or fragmentation. They compensate for losses from disease by producing vigorous new growth or sequester or compartmentalize the disease from spreading throughout the plant or plant population by vegetative fragmentation.

### 3.5. Matching host’s susceptibility with pathogen’s virulence

The importance of precise identification of the races or biotypes of arthropod biocontrol agents and their collection from the correct target biotype or subspecies has been stressed by several authors (e.g., Day and Urban, 2004; Harris, 1985). Proper host-agent matching is even more important for pathogen because, unlike insect herbivores, the host–pathogen specificity can be governed by single-gene differences or by a small number of genes, particularly at the subspecies level. Thus, a poor understanding of the taxonomy and genetic makeup of the target and/or the agent and the underlying host–pathogen relationship can cause temporary delays or even a permanent halt to biocontrol projects as a result of the agent’s unsatisfactory performance in assessment studies.

The importance of proper taxonomic background work to select the correct pathotypes for introduction became evident early on from the work on the *C. juncea–P. chondrillina* system in Australia (Burdon et al., 1981). Several distinct pathotypes of the rust occur in the native range of the host plant, skeletonweed, in the Mediterranean (Hasan, 1981). Many genotypes of the target weed also exist in the native range, with different levels of susceptibility to the prevalent rust strains (Espiau et al., 1998). In Australia, skeletonweed occurs as three asexual apomictic clones, designated A, B, and C, that can be distinguished by their leaf form as narrow, intermediate, and broad, respectively. The first rust strain released in Australia attacked only the narrow-leaf form. The epidemic that resulted from the introduced strain reduced the population density of the susceptible narrow-leaf form, while the other two, more resistant forms, became more widespread (Burdon et al., 1981). Additional rust strains virulent on the more resistant B and C clones were found and released (Hasan, 1985), but recent evidence suggests no measurable impacts of these strains against clones B and C (J. Cullen, CSIRO Entomology, Canberra, personal communication). Nonetheless, this is a remarkably successful project, with the benefit to cost ratio estimated at 100:1 to 200:1 (Cullen, 1985).

An isolate of the rust fungus *Maravalia cryptostegiae* (Cummins) Ono from Madagascar was released in Australia in 1993 to control rubbervine, *Cryptostegia grandiflora* Roxb. ex R.Br.; Apocynaceae (Tomley et al., 2003). Extensive host-range trials done under greenhouse conditions prior to the rust’s release indicated that it was virulent toward the Australian rubbervine. Yet, the released fungus registered a lower level of virulence in the field than anticipated (Evans and Tomley, 1996). A subsequent thorough taxonomic examination of the rust collections from their native range in Madagascar established that *M. cryptostegiae* exists in two physiological races, one adapted to *Cryptostegia* and the other to the closely related genus *Gonocryptha* (Evans, 1993). Under greenhouse conditions, differences in host specialization of these races were not clear on the host genotypes tested. With an understanding of the host specialization in the rust’s native habitats, coupled with taxonomic and pathogenicity studies, a more appropriate rust strain was found and released in Australia, resulting in a more effective control of the target, especially in wet years (Tomley et al., 2003).

Importance of proper host–pathogen matching was also highlighted in the work that led to the successful use of the rust fungus *Uromycladium tepperianum* (Sacc.) McAlpine as a classical biological control agent for *Acacia saligna* (Labill.) Wendl. in South Africa (Morris, 1991). Despite indications in older literature of a broad host range for this rust, the existence of distinct genotypes of *U. tepperianum* in Australia was confirmed by Morris (1991). The pathogen types differed in teliospore morphology and the ability to infect and produce galls only on hosts from which they were collected. Through careful matching of a highly virulent rust genotype with the South African *A. saligna* genotype, the program’s success was assured (Morris, 1997).

Bruckart et al. (1988) determined that the strain of the rust *Puccinia canaliculata* (Schw.) Lagerh. registered as the bioherbicide Dr. BioSedge (but never used commercially) was effective against some but not all regional biotypes of the target weed yellow nutsedge (*Cyperus esculentus* L.) in the United States. The registered rust strain was highly virulent on some yellow nutsedge types from the southeastern United States but not on types common in the Delaware-Maryland-Virginia area. Besides the problem of extremely narrow biotype specificity that restricted the potential usefulness of this rust strain, paradoxically it was found to infect a native sedge, *Cyperus fuscus* L., in the Netherlands, thus precluding it use as a classical biocontrol agent in Europe.
Another issue is the need to understand the extent of potentially useful genetic variability in a biocontrol pathogen. Tessmann (1999) assessed the virulence of nearly 70 isolates of Cercospora spp. isolated from diseased waterhyacinth (E. crassipes) leaves collected in South, Central, and North Americas, Africa, and the Caribbean. The isolates were found to vary widely in virulence as measured from the amount of foliar disease they caused; some caused only minor damage while others completely destroyed the leaf (pseudolamina). The standard bioherbicide candidate that had been extensively tested as a bioherbicide candidate, the isolate WH9BR (Charudattan et al., 1985), was only moderately virulent (10–25% damage) when compared to several newly found strains. Had a search for strains with higher levels of virulence been made in the native range of waterhyacinth at the beginning of the biocontrol project in Florida, a candidate with the highest virulence, and hence the highest potential for success, might have been chosen for further development. Yet, surveys during the initial search-and-screen phase typically do not aim to find the most virulent pathogen strains and researchers rarely, if at all, make supplementary surveys for this purpose. The tendency is to use a strain or strains on hand as the starting point for most projects. Not surprisingly, lack of efficacy of the agents is often cited as the primary reason for projects’ failure (Auld and Morin, 1995; Charudattan, 1991).

3.6. Practical and political considerations

Practical and political considerations are overriding factors in the selection of weed targets for control with pathogens. Demand from influential stakeholders for control or for a “nonchemical” or economically “sustainable” control typically provides the impetus to initiate as well as to continue pathogen-based biocontrol projects. However, stakeholders’ perceptions of the effectiveness and adequacy of biocontrol as a control option can be fickle. For instance, our project on biological control of waterhyacinth in Florida was driven by stakeholders’ desire to reduce the cost and amount of chemical herbicides used in the 1970s to manage this aquatic weed. Although an arthropod-based classical biological control program was well underway at this time, pathogens were sought as additional agents to tackle the seemingly intractable weed problem. However, by the 1980s, the waterhyacinth biocontrol program was declared a success; arguably, the weed had been brought under a significant level of control in the southeastern USA by two introduced curculionids, Neochetina eichhorniae Warner and N. bruchi Hustache. Nonetheless, during the ensuing decades, stakeholder perceptions of the adequacy of biocontrol as a management tool were at odds with those of the biocontrol’s supporters, prompting the State of Florida to adopt a chemical-herbicide-based “maintenance control program” as the best management strategy (Charudattan, 2001c; Haller, 1996; Joyce, 1985; Schardt, 1997).

Another important consideration is conflicts of interest. Theoretically, plant pathogens are ideal candidates as biocontrol agents for weeds, but their use is subject to conflicting interests, particularly with respect to their effects on nontarget species. The potential to increase background levels of inoculum in the environment, to expand host-range, and to cause long-term effects on agro- and natural ecosystems are aspects of regulatory and public concern (Barton, 2004; Bourdöt et al., 2004; Cook et al., 1996; Watson, 1985).

Syrett et al. (1985) and Turner (1985), among others, have categorized different types of conflicts that can affect the choice of weed targets. These relate to two basic issues: uncertain impacts and conflicting perspectives, which affect both insects and pathogens. The use of plant pathogens as weed-control agents creates another type of conflict—one between the traditional practitioners of plant pathology dedicated to the protection of plants from the ravages of pathogens and the biocontrol promoters’ view of pathogens as a weed-control resource. Because pathogens proposed as biocontrol agents may have nontarget hosts among crop plants or may have pathotypes that are crop pathogens, the plant-protection practitioners generally regard the use of pathogens for weed control with trepidation. Regulatory agencies likewise hold the view that pathogens used in weed control are “guilty until proven innocent” with regard to nontarget risks (William L. Bruckart, USDA-ARS FDWSRU, Ft. Detrick, MD, personal communication). Naturally, this notion can affect key issues such as permitting of pathogen importation, interstate movement of pathogens for research or use, and registration of bioherbicides. Whether or not this affects the choice of target selection, in my view, the pathogen-based projects generally suffer from this undercurrent of “fear factor.”

There are other examples where stakeholders have influenced the course of projects. Our project on classical biological control of waterhyacinth and milkweed vine (Morrenia odorata [Hook. & Arn.] Lindl.) using pathogens had to be abandoned due to unrealistic demands from the Technical Advisory Group (TAG) of that time. TAG sought data that could not be generated within a reasonable time frame and cost. The regulatory
posture towards pathogens at that time was deemed uninformed and unhelpful, prompting Freeman and Charudattan (1985) to decri the prevailing "pathophobia." Consequently, the project on waterhyacinth with the rust fungus *Uredo eichhorniae* Fragoso & Cifferi (Charudattan et al., 1976) and the other on milkweed vine with a newly discovered virus, Araujia mosaic potyvirus (Charudattan et al., 1980), were abandoned, the former temporarily and the latter permanently. In the case of the latter, the development and registration of the bioherbicide DeVine (*Phytophthora palmivora* [E.J. Butler] E.J. Butler; Table 2) was a further reason to abandon the classical biocontrol project.

A practical reality that affects the development of pathogens as bioherbicides is the competition from chemical herbicides. The stakeholders' familiarity with the chemical technology and its availability, affordability, and facility (compared to the less user-friendly bioherbicides) have largely discouraged stakeholder participation in many of the projects cited by Charudattan (2001a). Pathogens used as bioherbicides must be registered by the EPA as biopesticides, which adds a burden in regulatory costs and delays. Pathogens used in classical biological control, although by definition are 'biopesticides,' are regulated by USDA-APHIS: EPA needs only notification of APHIS' approval. Although this action is a mere formality, it does impose an extra step that pathogens must undergo.

Other practical considerations that can affect the course and outcome of programs include: (1) the availability of a prospective agent, as evidenced from published records and from field surveys. In the absence of encouraging findings in this regard, funding agencies are unlikely to continue support beyond a brief exploratory phase. (2) Once a promising project has been identified, further political and administrative support by the funding agencies, backed with an infusion of sufficient funds for the required duration to complete a project is also vital. Biological control programs are inherently slow and can stretch over several years; hence, they require broad support and cooperation from stakeholders over a long term, from the start to finish. Finally, (3) support from scientific peers in other competing weed control methods (e.g., chemical herbicides) is also critical. An appreciation for biological control among peers can lead to cooperation between chemical and biological control practitioners in their battle against weeds.

3.7. A case history

We are attempting to develop and register a tobamovirus, Tobacco mild green mosaic tobamovirus (TMGMV), as a bioherbicide to control tropical soda apple (*S. viarum*), a South American plant that is a highly invasive, noxious weed in Florida and the southeastern USA. Tropical soda apple (TSA) is of great concern from a regulatory standpoint because cattle shipped from Florida are implicated in spreading the weed into neighboring states. TSA also has established in several natural areas in Florida, posing significant concerns for environmental and natural resource management. These factors have prompted a strong stakeholder demand for control, a key to our selection of this weed as a target for biological control. Other considerations included the fact that the biocontrol agent we found, TMGMV, provided consistently high levels of control of TSA (>85% kill) and that it occurs naturally in Florida (Charudattan et al., 2004). Furthermore, TMGMV is principally a pathogen of plants in the Solanaceae and its plant-killing action is highly host-specific, being restricted to TSA and some cultivars of peppers (*Capsicum spp.*) and tobaccos (*Nicotiana spp.*) (Charudattan et al., unpublished). Unless susceptible pepper and *N. tabacum* L. cultivars are directly exposed to the virus during its application, which is unlikely, these nontarget plants will not be at risk. Since the virus has no natural vectors, its spread can be easily prevented through proper sanitation. Furthermore, the bioherbicide label can set safe distances from susceptible crops to mitigate potential risks to nontarget plants. Should any of the nontarget plants be affected, further damage can be altogether halted by temporary or permanent cessation of the virus' use. Therefore, further development and registration of TMGMV appears feasible. Thus, in this case, our choice of TSA as a weed target was driven by (1) stakeholder demand, (2) availability of a highly effective and feasible agent, and (3) an indication of economic viability of the bioherbicide product.

4. Conclusions

So what makes a good weed target for biological control by plant pathogens? I contend that a good target is one that has a strong stakeholder demand for control and the list of available pathogens suggests the possibility that satifying control can be obtained at a cost that is competitive with those of other available control options. Target selection will then be driven by a need for control as well as the availability of suitable pathogens. This need-driven target selection is applicable to insect biocontrols as well; nonetheless, with the history of scant funding for development of pathogens and the extra costs of technology-development and registration for bioherbicides, the pathogen-based weed biocontrol is clearly a market-driven enterprise.

The overall success rate (verifiable plus partial success; inoculative plus inudtative) of pathogen-based weed biocontrol projects is 17% (Table 1). Rather than dismissing the record of success with pathogens as being on the "low side," we should consider the potential for additive or synergistic effects by combining pathogen
and arthropod biocontrol agents. Might we see a success rate in the range of 50–100% if every project included both pathogens and insects has been advocated (Caesar, 2000, 2005)? I strongly second the proposal to include both pathologists and entomologists working in teams with a goal of integrating pathogens and insects for weed control. Such a team-approach to search for agents has been adapted in the program for Brazilian peppertree. *Schinus terebinthifolius* Raddi (Anacardiaceae) (J.P. Cuda, University of Florida, Gainesville, personal communication).

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