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Biological control of weeds by means of plant pathogens: Significance for integrated weed management in modern agro-ecology

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Abstract. Biological control of weeds by using plant pathogens has gained acceptance as a practical, safe, environmentally beneficial, weed management method applicable to agro-ecosystems. The interest in this weed control approach from public and private groups, and support for research and developmental effort, are on the upswing. This increasing interest is stimulated largely due to major economic, social, and environmental forces that are directing our choices in crop production practices. Some of these changes are market-driven while others are social and ecological in nature. These changes are in turn influencing the choices in weed control methods. In this regard, biocontrol with plant pathogens has been proven a feasible, albeit minor, component of modern integrated weed-management systems. This environmentally beneficial method should be promoted and exploited further to meet the current and future challenges in weed management in agro-ecosystems.

Key words: augmentation, bioherbicide, classical biocontrol, integrated weed management, plant pathogens, weed control

Introduction

Many excellent reviews of the topic of biological control of weeds by using plant pathogens have appeared in recent years; the readers are referred to articles by Auld and Morin (1995), Boyetchko (1999), Müller-Schärer et al. (2000), Rosskopf et al. (1999), and Watson (1991), among others. In this paper I will try to discuss the need and justification for continued investment in this field, significance of several recent developments, and raise some research priorities for further consideration.

Biocontrol with pathogens – need and justification

Although changes are a constant feature in modern agriculture, the recent confluence of several factors is affecting weed management practices and

consequently the agro-ecosystems in an unprecedented manner. The most notable changes include (1) the cancellation of the use of methyl bromide as a general purpose soil fumigant, (2) the phasing out of several older herbicides, (3) the high cost of developing and registering new chemical herbicides, (4) the lack of registered herbicides for small markets (e.g., minor use crops and aquatic [irrigation] systems), (5) the impact of herbicide-resistant crops on the use of other weed-control methods, (6) the public's resistance toward genetically altered food crops (e.g., herbicide-tolerant transgenic crops), (7) the increasing problems with herbicide-resistant weeds and weed-shifting, (8) government-instituted mandates for reducing chemical pesticide usage, (9) consumer preference for nonchemical alternatives in food production, (10) consolidation of agri-chemical companies, which affects the availability and marketing of certain chemical herbicides, and (11) shifts in agricultural production from small and medium operations to large corporate operations and from high-cost to low-cost production areas of the world, following a pattern of globalization of agricultural production and marketing. Singly and collectively, these changes have a profound impact on weed management practices, and I expect this evolving situation to create a renewed interest and demand for biological controls. Such renewal is already evident in the United States in the number of new opportunities for research and development of biologically based pest control alternatives. The potential of plant pathogens as weed control agents – both as conventional biocontrol agents and as sources of genes and genetic mechanisms controlling plant mortality – is too great not to continue our investment in this field of endeavor. Also, in some situations (e.g., alpine pastures [Ammon and Müller-Schärer, 1999], managed and natural forests, and some waterways) only one dominant weed species needs to be managed and this must be done without reducing the species richness of the flora and fauna. Therefore, a high level of selectivity is needed – a situation ideal for biological control.

For the purpose of this paper, agro-ecosystem is broadly defined to include crops and crop lands, managed and natural pastures and rangelands, managed plantations and agroforests, and certain waterways that supply irrigation water. All of these systems and sites are subject to weed problems, and biological control programs should consider all applicable strategies for using plant pathogens (classical, inundative, and augmentative strategies) rather than follow the historic precedence of relying on the inundative (bioherbicide) approach to manage weeds in intensively managed systems versus classical approach to tackle weeds in unmanaged systems. For example, weeds such as *Senecio vulgaris*, *Portulaca oleracea*, *Senna obtusifolia*, *Amaranthus* spp., *Avena fatua*, and many others, occur both in agricultural lands and the surrounding areas. Biocontrol programs that aim to control these weeds only

in the agricultural fields are likely to fail since these weeds can reinfest the fields from uncontrolled surrounding populations. Therefore, it would be prudent to combine classical, inundative, and/or augmentative biocontrol strategies, depending on the situation. With this in view, the following discourse covers examples of pathogens used in classical, inundative, and augmentation strategies rather than focus simply on the inundative strategy.

Recent history and contribution to weed management systems

Since 1980, eight bioherbicides have been registered worldwide, and at least 15 new introductions of classical biocontrol agents have occurred, including one that can be regarded as a highly successful example (see below, the discussion on *Uromycladium tepperianum*; Morris et al., 1999). These biocontrol agents join the ranks of other successful programs that predate 1980 (see Table 1 for names of pathogens, weeds, and other details). In addition, there has been a recent demonstration of the potential to use a pathogen as an augmentative agent in a system-management approach (Müller-Schäler and Frantzen, 1996; see below). Notwithstanding these accomplishments, the overall contribution of biological control to meet the worldwide needs in weed control remains very small, considering the limited number of pathogens used to manage a short list of weeds among the myriads that need to be controlled. However, a parallel argument is also justified: plant pathogens are one of several tools available to us in our constant efforts to fine-tune modern weed management systems. To overlook any potential tool would be unwise, considering the diversity of weed problems and weed control needs that exist. In situations where pathogens have been used to control weeds, the accrued benefits to the users have been substantial and highly significant such as a 100:1 to 200:1 benefit to cost ratio estimated for the Australian biocontrol program on *Chondrilla juncea* (Cullen, 1985; Marsden et al., 1980). Also, the success ratio of the number of prospective agents screened to the number put into practical use is highly favorable in the case of pathogens compared to chemical herbicides. Typically, the discovery and commercialization process for chemical herbicides starts with literally thousands of compounds, but with a success rate of less than 1%. On the contrary, a conservative estimate of the success ratio of the number of pathogens studied to the number used regularly or intermittently by users is 20:1 (calculated from an analysis of data in Charudattan, 1991 and Table 1). This cost-benefit analysis becomes even more favorable for bioherbicides when we consider the capital outlays needed for research, development, and registration of chemical herbicides versus bioherbicides, said to be in the range of US$ 50 million for chemical herbicides versus US$ 2 million for bioherbicides (author's estimate).

Table 1. Examples of pathogens used as weed biocontrol agents

Weed	Pathogen (Registered name)	Target crop(s) or sites	Country[a]	A reference to the agent and/or location
As classical biocontrol agents: Documented and verifiable successes				
Acacia saligna	*Uromycladium tepperianum*	Natural sites	South Africa	Morris, 1999
Ageratina riparia	*Entyloma ageratinae*	Rangelands; forests	Hawaii, USA;	Trujillo et al., 1988; Barreto and Evans, 1998
			South Africa	Morris, 1991
Chondrilla juncea	*Puccinia chondrillina*	Wheat; rangelands	Australia	Hasan, 1981
Rubus spp.	*Phragmidium violaceum*	Natural sites; farmlands	Chile	Oehrens, 1977
As classical biocontrol agents: Some success achieved or results promising; further documentation needed				
Acroptilon repens	*Subanguina picridis*	Rangelands; natural sites	Canada; USA; Azerbaijan	Parker, 1991
Ageratina adenophora (=*Eupatorium adenophorum*)	*Phaeoramularia eupatorii-odorati* (previously referred to as *Cercospora eupatorii*)	Natural sites; urban sites	Australia; New Zealand South Africa	Dodd, 1961; Hill, 1989; Morris et al., 1999
A. riparia	*Entyloma ageratinae*	Natural areas	New Zealand	Fröhlich et al., 1999b
Ambrosia artemisiifolia	*Albugo tragopogonis*	Natural sites; farmlands	Russia	Julien and Griffiths, 1998
Baccharis halimifolia	*Puccinia evadens*	Rangelands; natural sites	Australia	Charudattan et al., 1995
Carduus thoermeri	*Puccinia carduorum*	Rangelands; natural sites	USA	Luster et al., 1999
Chondrilla juncea	*Puccinia chondrillina*	Wheat; rangelands	Argentina	Julien and Griffiths, 1998
			USA	Supkoff et al., 1988
Clidemia hirta	*Colletotrichum gloeosporioides* f.sp. *clidemiae*	Forest lands	Hawaii, USA	Trujillo et al., 1986
Cryptostegia grandiflora	*Maravalia cryptostegiae*	Rangelands; natural sites	Australia	Tomley and Evans, 1996

Mimosa pigra	*Sphaerulina mimosae-pigrae* (anamorph: *Phloeospora mimosae-pigrae*)	Coastal flood plains	Australia	Forno et al., 1996
Passiflora tripartita; *P. mollissima*	*Septoria passiflorae*	Natural sites	Hawaii, USA	Julien and Griffiths, 1998
Rubus spp.	*Phragmidium violaceum*	Natural sites; farmlands	Australia	Bruzzese, 1995
Xanthium occidentale	*Puccinia xanthii*	Natural areas; farmlands	Australia	Morin et al., 1996
As classical biocontrol agents: Agent released intentionally or accidentally; impacts uncertain				
Acroptilon repens	*Puccinia acroptili*	Natural sites	Canada	Mortensen and Molloy, 1989
Carduus tenuiflorus	*Puccinia carduorum*	Natural sites; rangelands	USA	Baudoin et al., 1993
Carduus pycnocephalus	*Puccinia cardui-pycnocephali*	Natural sites	Australia	Julien and Griffiths, 1998
Chondrilla juncea	*Puccinia chondrillina*	Natural sites; rangelands	Canada	Julien and Griffiths, 1998
Cirsium arvense	*Puccinia punctiformis* (=*P. obtegens*)	Natural sites; rangelands	Australia; Canada; New Zealand; USA	Julien and Griffiths, 1998
Clematis vitalba	*Phoma clematidina*	Natural sites	New Zealand	Gourlay et al., 1999
Echium plantagineum	*Cercospora echii*	Natural sites; rangelands	Australia	Floyd et al., 1996
Eichhornia crassipes	*Cercospora piaropi* (=*C. rodmanii*)	Waterways	South Africa	Morris et al., 1999
Galega officinalis	*Uromyces galegae*	Natural sites; farmlands	Chile	Oehrens and Gonzales, 1975
Heliotropium europaeum	*Uromyces heliotropii*	Natural sites	Australia	Delfosse et al., 1995
Hypericum androsaemum	*Melampsora hypericorum*	Natural sites	Australia	Casonato et al., 1999
Mimosa pigra	*Diabole cubensis*	Coastal flood plains	Australia	Seier and Evans, 1996
Parthenium hysterophorus	*Puccinia abrupta* var. *partheniicola*	Natural areas	Australia	Parker et al., 1994
As inundative (bioherbicide) agents: Registered and/or commercially available agents[b]				
Acacia spp.	*Cylindrobasidium laeve* (Stumpout, Plant Protection Research Institute)	Tree plantations	South Africa	Morris et al., 1999

Table 1 (continue)

Weed	Pathogen (Registered name)	Target crop(s) or sites	Country[a]	A reference to the agent and/or location
Aeschynomene virginica	*Colletotrichum gloeosporioides* f.sp. *aeschynomene* (Collego; Encore Technologies)	Rice and soybean	USA	TeBeest et al., 1992
Broad-leaved trees	*Chondrostereum purpureum*[c] (BioChon; Koppert)	Tree plantations	The Netherlands	de Jong et al., 1990
Cyperus esculentus	*Puccinia canaliculata* (Dr. BioSedge)	Various crops	USA	Phatak, 1987
Hakea sericea	*Colletotrichum gloeosporioides* (Hakatak)[d]	Natural sites	South Africa	Morris et al., 1999
Malva pusilla and *Malva* spp.	*Colletotrichum gloeosporioides* (previously registered as BioMal by PhilomBios and Agriculture and Agri-Food Canada, but now defunct; proposed new product: Mallet WP, Encore Technologies, registration expected in the USA in 2001-2002)	Various crops	USA; Canada	Mortensen, 1996; D.R. Johnson, Encore Technologies, personal communication
Morrenia odorata	*Phytophthora palmivora* (DeVine; Abbott Laboratories)	Citrus	USA	Ridings, 1986
Poa annua	*Xanthomonas campestris* pv. *poae* (Camperico; Japan Tobacco)	Golf courses; turf grass	Japan	Imaizumi et al., 1997
	As inundative (bioherbicide) agents: Promising agents for further development[e]			
Abutilon theophrasti	*Colletotrichum coccodes*	Various crops	Canada	DiTommaso et al., 1996
Alternanthera philoxeroides	*Nimbya alternantherae*	Waterways; wetlands	Brazil-USA	Barreto et al., in press
Amaranthus spp.	*Phomopsis amaranthicola*	Vegetables	USA	Rosskopf, 1998
	Alternaria alternata	Various crops	Europe	Bürki et al., 2000
	Trematophoma lignicola			

Avena fatua	*Drechslera avenacea*	Various crops	Australia-Italy	Vurro et al., 1999
Calystegia sepium	*Stagonospora convolvuli*	Various crops	Europe	Guntli et al., 1999
Cirsium arvense	*Pseudomonas syringae* pv. *tagetis*	Various crops; natural areas	USA	Johnson et al., 1996
	Phomopsis cirsii	Various crops	Europe	Leth and Andreasen,1999
Chenopodium album	*Ascochyta caulina*	Various crops	The Netherlands	Scheepens et al., 1997
Convolvulus arvensis	*Stagonospora convolvuli*	Various crops	Europe	Pfirter et al., 1997
Cuscuta spp.	*Alternaria destruens* (pending possible registration in USA in 2001)	Cranberries	USA	T.A. Bewick, Univ. Massachusetts, personal communication
Cyperus rotundus	*Dactylaria higginsii* (=*Pyricularia higginsii*)	Various crops	USA; Israel	Kadir and Charudattan, 2000 Dinoor et al., 1999
	Cercospora caricis	Various crops	Brazil; Israel	Ribeiro et al., 1998; Dinoor et al., 1999
Cytisus scoparius	*Fusarium tumidum*	Tree plantations	New Zealand	Fröhlich et al., 1999a
Echinochloa crus-galli; *Echinochloa* spp.	*Exserohilum fusiforme; E. monoceras* *Colletotrichum graminicola*	Various crops	Vietnam-Australia Canada; South Korea	Van Tuat et al., 1998; Zhang and Watson, 1997; Yang et al., 2000
Egeria densa; E. najas	*Fusarium* sp.	Hydroelectric reservoirs	Brazil	Nachtigal and Pitelli, 1999
Eichhornia crassipes	*Cercospora piaropi*	Waterways, lakes, irrigation	USA	Vincent and Charudattan, 1999
	Alternaria eichhorniae	canals, etc.	Egypt	Shabana et al., 1999
Erythroxylum coca	*F. oxysporum* f.sp. *erythroxyli*	Coca plantations	Coca producing regions	Hebbar et al., 1999; Sands et al., 1997
Euphorbia heterophylla	*Bipolaris euphorbiae*	Various crops	Brazil	R.A. Pitelli, personal communication
Galinsoga ciliata; *G. parviflora*	*Colletotrichum gloeosporioides*	Various crops	Russia	Gasich and Titova, 1998
Hakea sericea	*Colletotrichum gloeosporioides*	Tree plantations	South Africa	Morris et al., 1999

Table 1 (continue)

Weed	Pathogen (Registered name)	Target crop(s) or sites	Country[a]	A reference to the agent and/or location
Hedychium gardnerianum	*Ralstonia solanacearum*	Forests	Hawaii, USA	Anderson and Gardner, 1999
Imperata cylindrica	*Colletotrichum caudatum*	Various crops	Malaysia	Caunter and Lee, 1996
	Bipolaris sacchari; *Drechslera gigantea*	Natural sites; forests; roadsides	USA	Yandoc et al., 1999
Orobanche spp.	*Fusarium oxysporum*	Cereal crops; various crops	Sudan-Germany	Kroschel et al., 1999
Rottboellia chochinchinensis	*Sporisorium ophiuri*	Cereals	Thailand-UK	Reeder et al., 1996
	Colletotrichum graminicola			
Sagittaria spp.	*Rhynchosporium alismatis*	Rice	Australia	Cother et al., 1999
Senna obtusifolia	*Alternaria cassiae*	Soybean	Brazil	R.A. Pitelli, personal communication
Sesbania exaltata	*Colletotrichum truncatum*	Soybean and rice	USA, Mississippi	Boyette et al., 1999
Solanum viarum	*Ralstonia solanacearum*	Citrus and sod	USA, Florida	DeValerio et al., 2000
Sphenoclea zeylanica	*Alternaria* sp.	Rice	Philippines	Masangkay et al., 1996
	Colletotrichum gloeosporioides	Rice	Malaysia	Caunter and Lee, 1996
Striga hermonthica	*Fusarium nygamai*	Various crops	Sudan-Germany	Kroschel et al., 1999
	Fusarium oxysporum		West Africa-Canada	Ciotola et al., 1995
	Fusarium semitectum var. *majus*			
Taraxacum officinale	Fungal isolate MAC 1	Lawns; gardens	Canada	Schnick et al., 1998
Trianthema portulacastrum	*Gibbago trianthemae*	Various crops	India	Aneja et al., 1999
Ulex europaeus	*Fusarium tumidum*	Plantation crops	New Zealand	Fröhlich et al., 1999a
Various annual weeds	*Myrothecium verrucaria*	Various crops	USA, Maryland	Walker and Tilley, 1997
Various weedy grasses	*Drechslera gigantea; Exserohilum longirostratum; E. rostratum*	Citrus; other tree crops	USA	Chandramohan, 1999

Pueraria lobata	*Myrothecium verrucaria*	Roadsides; natural areas	USA	C.D. Boyette, USDA-ARS, Stoneville, MS, personal communication
	Pseudomonas syringae pv. *phaseolicola*			Zidack and Backman, 1996
Various broad-leaved trees	*Chondrostereum purpureum*	Agroforestry	Canada; USA	Harper et al., 1999
Various weeds in Asteraceae	*Pseudomonas syringae* pv. *tagetis*	Various crops	USA; Canada	Johnson et al., 1996
Various weeds	*Sclerotinia sclerotiorum*	Various crops	Australia; New Zealand; USA	Sands et al., 1990
Xanthium spp.	*Alternaria zinniae*	Various crops	Australia; USA	Auld et al., 1992; Abbas, 1998
	Colletotrichum orbiculare	Various crops	Australia	Auld et al., 1990
	As augmentative agents: Agents that could be developed for a system-management approach			
Amaranthus retroflexus	*Albugo amaranthi*	Various crops	Europe	Jüttersonke, 1998
Cyperus esculentus	*Puccinia canaliculata*	Various crops	USA	Phatak et al., 1987
C. rotundus	*Puccinia romagnoliana*	Various crops	India; Israel	Bedi and Grewal, 1999; A. Dinoor, Hebrew Univ. of Jerusalem, Israel, personal communication
Senecio vulgaris	*Puccinia lagenophorae*	Various crops	Europe	Müller-Schärer and Frantzen, 1996
Sorghum halepense	*Sporisorium cruentum* (=*Sphacelotheca holci; S. cruenta*)	Various crops	USA	Massion and Lindow, 1986
Rosa multiflora	Rose rosette disease	Farmlands	USA	Epstein et al., 1997
Rottboellia chochinchinensis	*Sporisorium ophiuri*	Cereal crops	UK	Reeder et al., 1996

Table 1 (continue)

Weed	Pathogen (Registered name)	Target crop(s) or sites	Country[a]	A reference to the agent and/or location
	For integrated weed management systems using pathogens or plant-associated microbes and insects			
Eichhornia crassipes	*Acremonium zonatum; Alternaria eichhorniae; Cercospora piaropi*; *Neochetina bruchi; N. eichhorniae*; other insects	Waterways, lakes, irrigation canals, etc.	Egypt; South Africa; USA	Den Breeÿen, 1999; Vincent and Charudattan, 1999; Shabana et al., 1999
Euphorbia esula	*Fusarium* spp.; *Rhizoctonia* spp.; *Aphthona* spp.; other insects	Natural sites; rangelands	USA	Caesar, 1999
Various weeds	Rhizobacteria as weed-suppressive agents	Various sites	USA; Canada	Kremer and Kennedy, 1996; Boyetchko et al., 1999

[a]Country or countries where the agent is used or intended to be used. Countries linked by a hyphen are engaged in a cooperative program; countries separated by a semicolon are engaged in independent work on the agent(s). Compiled from published reports. [b]Name of the commercial product and its manufacturer/seller are given in brackets. [c]A C. *purpureum*-based product, EHONTROL, is under evaluation for registration in Canada and the USA (Harper et al., 1999; Gosselin et al., 1999). [d]A provisional registration, granted in 1990, lapsed in 1991 due to lack of commercial interest. A dried spore preparation, available through the Plant Protection Research Institute, Stellenbosch, is being supplied to a small but increasing number of users (Morris et al., 1999). [e]These examples were selected based on the economic importance of the weed target and published accounts of the agents' effectiveness and potential for further development.

Despite this favorable outlook, the number of researchers and the number of weeds targeted for classical biocontrol by pathogens have been quite modest during the past 30 years. It is hard to estimate the exact numbers of scientist-years (SY) assigned to classical biocontrol projects (using pathogens) at any given time since many scientists divide their efforts between classical and bioherbicide projects and between research and other duties. In my liberal estimate, an average of 2.5 SYs per year has been assigned in the USA, 1.5 in Australia, 1.5 in UK, 1.0 in South Africa, 0.5 in Brazil, 0.5 in Canada, and 0.5 in New Zealand, for example. This investment in classical biocontrol is indeed quite modest compared to the number of potential weed-pathogen systems that merit attention. A reason for this limited input is that classical biocontrol programs require cooperation and coordination at all levels from various governmental agencies and institutions. Initiatives to develop and fund research are often lacking except in a few countries with a history of involvement in biocontrol. Furthermore, the process of discovery to implementation of classical biocontrol, by its nature, is slow and requires a decade or more from the start to produce tangible results. Administrative and funding support for such a long-term weed control approach is generally difficult to justify except in a few programs. Coupled with this, the public's perception of risks to nontarget plants from classical biocontrol introductions, epitomized by the recent controversy surrounding the thistle-head weevil *Rhinocyllus conicus* (Louda et al., 1997) could lead to an unjust tendency to be over-cautious in the initiation and implementation of some programs.

Compared to classical biocontrol, bioherbicides (inundative use of pathogens) have enjoyed better support and greater involvement by scientific groups in several countries during this period, involving about 25 SYs worldwide per year in about 25 separate groups. In addition, the regulatory climate in the United States for the development and registration of bioherbicides under the 'green labeling' or 'biopesticide' protocols has never been more favorable. Several new funding initiatives, such as the programs in the USA on invasive weeds, nonchemical pest control alternatives, integrated pest management, food-quality protection, methyl bromide alternatives, etc. are providing a stimulus to biocontrol.

Interest in the augmentation strategy has been also sparse during the last 20 years. Except for a couple of notable studies (Massion and Lindow, 1986; Phatak et al., 1987), there has been a general lack of research initiatives in this area. Understandably, the availability of cheap and effective chemical herbicides has been a disincentive for the development and implementation of a system-based control strategy (i.e., the systems needed to conserve and augment biocontrol agents). Hopefully, this situation is changing with the

recent initiation in Europe of a program to explore the utility of a system-management approach (Müller-Schärer and Frantzen, 1996; see below).

A handful of cooperative regional research programs and binational programs are currently underway in which scientists from different regions and/or countries are cooperating to find pathogens to control weeds of common interest. These are: the European COST project 816 (European Cooperation in the Field of Scientific and Technical Research, Biological Control of Weeds in Crops); the US projects S-267 (Biological Control of Selected Arthropod Pests and Weeds, focused on classical biological control) and S-268 (Evaluation and Development of Plant Pathogens for Biological Control of Weeds, emphasizing bioherbicides); the Brazil-University of Florida cooperative program; the Philippines-Macdonald College, Quebec, Canada program; the Australia-Vietnam project on grass weeds sponsored by the Australian Centre for International Agricultural Research; the German-Sudan project on parasitic weeds sponsored by the German Institution for Technical Cooperation; the ICRISAT-sponsored *Striga* project in Western Africa (Mali and Niger); and the recently formed Pan-African project to develop mycoherbicides to control *Eichhornia crassipes* in African countries. In addition, there is a substantial investment in biocontrol of weeds in projects supported by agencies such as US Department of Agriculture-Agricultural Research Service, Agriculture and Agri-Food Canada, Forestry Canada, CABI Biosciences (UK), the Council of Scientific and Industrial Research Organization (Australia), Landcare Research (New Zealand), and several regional (state or provincial) agencies. A few private companies in Japan and the USA also conduct in-house research on bioherbicides.

Bioherbicides: How have they fared?

Since the bioherbicide strategy has enjoyed better support and more scientific study than classical and augmentation methods, it is reasonable to ponder the outcome of nearly three decades of investment in this field. Accordingly, an analysis of the commercially available bioherbicides has led me to the following generalizations.

Typically, each bioherbicide is used in a highly specific manner to control a single weed species. The Collego (*Colletotrichum gloeosporioides* f.sp. *aeschynomene*) and DeVine (*Phytophthora palmivora*) models are in this category. A few experimental, but not yet practical, attempts have been made to combine two or more pathogens to control one or more weeds (Boyette et al., 1979; Den Breeÿen, 1999; Hallett et al., 1995; Morin et al., 1993). The objectives of these attempts have been either to increase the level of control of a difficult-to-control weed or to increase the number of weeds controlled with a single application. Recently, the feasibility of controlling

several weeds with a cocktail of three pathogens has been demonstrated in the field (Chandramohan, 1999; Chandramohan et al., 2000). While the use of a highly host-specific pathogen to control a single weed species would be mandatory in a classical biocontrol system, the absence of broad-spectrum bioherbicides is simply the result of a regulatory mind-set that required that bioherbicide agents should possess sufficiently narrow host ranges. In fact, many facultative parasites, such as *Alternaria cassiae, Chondrostereum purpureum, Colletotrichum gloeosporioides, Cylindrobasidium levae, Dactylaria higginsii, Phomopsis amaranthicola, Pseudomonas syringe* pv. *tagetis*, and *Sclerotinia sclerotiorum*, to name a few, that are either registered or being developed as bioherbicides, do not have very high levels of host specificity comparable to that of rust fungi and therefore, hypothetically, could be used against more than one weed species (e.g., *D. higginsii* for *Cyperus* spp., *P. amaranthicola* for *Amaranthus* spp., *P. syringae* pv. *tagetis* to control several weeds in Asteraceae and other families, and pathogen cocktails to control several taxonomically distinct weeds).

The existing commercial bioherbicides are all used on a relatively small scale (a maximum of few thousand hectares) and on a regional (one or two states or provinces) or local (a few counties) basis. Hence, the market value of bioherbicides is relatively modest compared to chemical herbicides, said to be not more than $200,000 to $500,000 per biocontrol agent per year (anonymous industry sources). It is hoped that some weeds of worldwide importance, such as *Amaranthus* spp., *Cyperus* spp., *Echinochloa crus-galli, Portulaca oleracea*, weedy grasses, and others may provide for larger returns and hence generate sufficient economic incentives for development of commercial bioherbicide products.

Analogous to the situation with other pest control products, the bioherbicides are used in conjunction with other pest control and crop management products (insecticides, fungicides, herbicides, and other agrochemicals) and weed-control methods (chemical control, cultivation, and crop competition). Thus, bioherbicides have been used as components of integrated weed management systems (Smith, 1991) rather than as standalone options. This feature will continue to be key to the public's acceptance of bioherbicides.

Significance of contributions

A list of pathogens that are currently in use or undergoing testing in a precommercial or prerelease phase is given in Table 1. The following is a synopsis of some major accomplishments.

Classical biocontrol agents

Since the 1980s, at least one documented example of a highly successful classical biocontrol program has occurred, namely, the control of *Acacia saligna* by the rust fungus *Uromycladium tepperianum* introduced into South Africa from Australia. *Acacia saligna* is regarded as the most important invasive weed in the Cape Fynbos Floristic Region of South Africa. The fungus causes extensive gall formation on branches and twigs, and heavily infected branches droop and the tree is eventually killed. The fungus was introduced into the Western Cape Province between 1987 and 1989, and in about eight years the rust disease became widespread in the province and tree density has decreased by 90–95%. The number of seeds in the soil seed bank also stabilized in most sites and the process of tree decline is continuing (Morris, 1999). Considering the negative impact of the weed on the unique ecosystem, the impact of the gall rust on the tree populations, the value of *A. saligna* as fire wood, and alternative land uses, it has been determined that the benefits of this biocontrol program far outweigh the potential loss of social benefits, mainly as fire wood, to be derived from this invasive tree species (Morris, 1999).

In another example, *Puccinia carduorum*, imported from Turkey and released into the USA to control musk thistle, *Carduus thoermeri*, has spread widely from its original introduction in the northeastern United States (states of Virginia and Maryland) to Wyoming and California in the west (Bruckart et al., 1996; Luster et al., 1999). Studies indicate that *P. carduorum* can indeed significantly reduce musk thistle density (Baudoin et al., 1993) and the effects of this fungus on insect biocontrol agents of this weed are negligible (Kok et al., 1996).

Two other rust fungi, *Maravalia cryptostegiae* and *Puccinia evadens*, introduced into Australia from Madagascar and Florida, USA, respectively, to control *Cryptostegia grandiflora* and *Baccharis halimifolia*, are beginning to have significant impacts on the densities of their respective weed hosts (Rachel McFadyen, Queensland Department of Lands, Australia, personal communication). Other classical introductions that appear to be producing successful results include *Entyloma ageratinae* on *Ageratina riparia* in New Zealand (previously used successfully in Hawaii on this weed; see Table 1) and *Sphaerulina mimosae-pigrae* (anamorph: *Phloeospora mimosae-pigrae*) on *Mimosa pigra* in Australia.

Bioherbicides

Among the eight bioherbicides approved for use, with or without registration as a ‘pesticide’ (Table 1), two, BioMal (*Colletotrichum gloeo-*

sporioides f.sp. *malvae*) and Dr. BioSedge (*Puccinia canaliculata*), have been unavailable for commercial use since their registration due to economic considerations or lack of suitable production methods. The former agent is currently under development by Encore Technologies, Minnetonka, MN, under the commercial name of Mallet WP, a different formulation from BioMal. Mallet is effective against round-leaved mallow (*Malva pusilla*) and small flowered mallows (*Malva* spp.) (D.R. Johnson, Encore Technologies, personal communication). Hakatak (*Colletotrichum gloeosporioides*) was provisionally registered until commercial interest in this bioherbicide ceased; however, a bioherbicide preparation consisting of dry spores is still available to interested users (Morris et al., 1999).

In addition to the above-mentioned products, which represent a tangible output from this field, the contributions of scientific knowledge, i.e., to our understanding of weed-pathogen systems, epidemiology of classical, inundative, and augmentative techniques, microbial ecology of aerial and soil environments of plants, microbial mass-production systems, formulation technology, and molecular biology of some biocontrol agents, have been highly useful and significant. The reasons for the lack of a greater success (i.e., more successful examples) are many, as aptly stated by Auld and Morin (1995).

In general, the above-mentioned bioherbicides have been developed and registered/approved following the 'pesticide paradigm'. For example, each of the two bioherbicide prototypes, Collego and DeVine, consists of a single, highly effective fungal pathogen that is applied with or without amendments/formulations as an aerial, postemergent spray (TeBeest et al., 1992). This model is also followed in the case of Camperico (*Xanthomonas campestris* pv. *poae*) (Imaizumi et al., 1997). Whereas a preapplication mowing is integral to the application of Camperico, BioChon (*Chondrostereum purpureum*) and Stumpout (*Cylindrobasidium levae*) are applied by 'painting' the bioherbicide preparation to cut tree stumps (de Jong et al., 1990; Morris et al., 1999). Hakatak can be applied as aerially broadcasted pellets or by wound inoculation of a liquid spore suspension (Morris et al., 1999). Dr. BioSedge, which is registered in the USA as a bioherbicide, fits more appropriately the augmentation strategy for two reasons: the amount of inoculum needed to initiate a well-timed epidemic of this rust disease is only 2.5 to 5 mg of uredospores per hectare, and it is possible to apply this fungus through center-pivot irrigation systems or by natural wind-borne dissemination from an inoculum source, as opposed to the targeted application used in the case of Collego and DeVine (Phatak et al., 1987).

Some important innovations have also been made during the last decade in the areas of inoculum production, formulation of agents, and application

methods. In addition, a few novel (i.e., previously untested, although the ideas may not be new) approaches have been developed and tested to improve the number of weeds that could be targeted for control with a single agent (i.e., broad-spectrum activity) or a single application (i.e., multiple pathogens applied as a cocktail). Finally, several effective bioherbicide candidates for weeds of global significance are undergoing evaluation for possible commercial/practical use. Some of the important innovations and agents are as follows.

Production

Commercialization of bioherbicides requires economically feasible methods of production of the bioherbicide agents (Churchill, 1982; Stowell, 1991). In the case of fungi, the preferred method of industrial production is by means of liquid fermentation, but many fungi do not produce spores under submerged conditions. In this case, a biphasic production system, wherein a fungus is first cultured in liquid shake cultures, followed by slow drying in a shallow layer (Walker, 1980; Chandramohan and Charudattan, 1998) or over solid support (Stowell, 1991), have been shown to be practical. Use of natural substrates like grains, weed seeds, and other plant tissues (Ciotola et al., 1995; Yandoc and Charudattan, 1998; Wyss et al., 1999; R.A. Pitelli, University of the State of Sao Paulo, Jaboticabal, personal communication) may offer an economical and facile low-technology method of spore production. Basidiomycetes such as *Chondrostereum purpureum* and *Cylindrobasidium levae* can be produced as infective mycelia in liquid culture or on sterilized wood blocks (Morris et al., 1999). Amsellem et al. (1999) have developed a method to produce stable mycelial inocula of *Fusarium arthrosporioides* and *F. oxysporum* that could be stored without loss of infectivity for more than 9 months. Adoption of the solid-substrate production methods used in the mushroom-spawn industry is another commercially feasible option.

Jackson et al. (1996) have demonstrated that the fitness (survival and infectivity) and propagule types produced by *Colletotrichum truncatum* in liquid-fermentation cultures can be greatly influenced by the carbon-to-nitrogen ratio. This and numerous other studies in microbial fermentation literature would indicate beyond question that the survival, virulence, metabolite production, etc. of microorganisms can be controlled by nutritional quality, agitation and aeration rates, pH, temperature, and other parameters of the medium (Churchill, 1982; Stowell, 1991). Given this fact, production systems for bioherbicides must, by necessity, remain an art and an empirical process. Therefore, major breakthroughs in this area can occur only by following the present course of examination of pathogens on a case-by-case basis.

Compared to fungal bioherbicides, bacterial pathogens such as *Xanthomonas campestris* pv. *poae* and *Pseudomonas syringae* pv. *tagetis* are very easy and quick to produce in liquid cultures and to store as frozen or freeze-dried pellets (Imaizumi et al., 1997; Johnson et al., 1996). Even simpler to produce, store, and use are mechanically transmitted viruses like *Araujia mosaic virus* and *Tobacco Mild Green Mosaic Virus* U2 (Charudattan et al., 1980; Pettersen et al., 2000), which can be multiplied on tolerant (nonlethal) hosts, freeze-dried, and stored for several years without loss of infectivity.

Formulation

The topic of bioherbicide formulations has been reviewed in many recent articles (Boyetchko et al., 1999; Boyette et al., 1996; Daigle and Connick 1990; Connick et al., 1998; Greaves et al., 1998; Green et al., 1998). An assessment of the literature reveals that four types of materials/formulations have received much attention: various kinds of emulsions, organosilicone surfactants such as Silwet L-77, hydrophilic polymers, and alginate-, starch-, cellulose-, or gluten-based encapsulation systems. Each of these types has its specific advantage as well as disadvantage. Emulsions can be constituted to predispose weeds to bioherbicide agents and thereby improve the efficacy and consistency of weed control. Some surfactants, such as Silwet L-77, can facilitate direct entry of small cells (bacterial cells and small spores) into the weeds' tissues. Hydrophilic polymers, as a broad group, include numerous types of natural and synthetic polymers with different levels of water-holding qualities. Encapsulation methods offer possibilities to apply bioherbicides as dry material, to soil, water, and aerial plant surfaces. On the negative side, formulations composed of expensive materials or those that require technical sophistication are bound to increase the cost of bioherbicide products. Moreover, some materials used in these formulations may not be acceptable from a toxicological perspective. Furthermore, the formulation type will also affect the choice of application tools and methods; for example certain emulsions cannot be applied by conventional sprayers used by farmers.

As stated by Greaves et al. (1998), innovations in formulation technology are vital if we are to succeed with the next generation of bioherbicides. However, for best results, the pathogen should be inherently virulent or possess a potent weed-killing phytotoxin. The formulation should predispose the weed to infection by the pathogen or it should strongly buffer the pathogen propagules against environmental constraints while promoting disease development. Thus, research efforts must first aim to discover and develop only those pathogens that are highly destructive and have a

reasonable chance of succeeding under field conditions (Charudattan, 1988; Mortensen, 1985).

Application technique

As stated, Collego and DeVine are applied with conventional application tools and methods: with land-based or aerial sprayers (TeBeest et al., 1992). Some attempts have been made to apply foliar pathogens through soil or on the surface of soil, as broadcasted pellets or in-row applications (Pitelli et al., 1994; Weidemann and Templeton, 1988), but these methods generally have not been put into practical use. Thus, the preferred method of application is clearly by postemergent spraying with conventional sprayers. Likewise, most evaluations in the laboratory have used aerosol sprayers, hand-pumped sprayers, and pressurized sprayers propelled by CO_2 or compressed air. The field applicators produce a wide range of droplet sizes and usually are operated at application volumes of less than 250 l/ha to 500 l/ha. Studies using a fluorescein dye to measure spray retention on *Amaranthus retroflexus* suggested that there can be a loss of at least 84% of the formulated spores between the time the spray is discharged to the final retention on the leaf. An examination of spore deposition, spore germination, and lesion development on leaves indicated that there was only 8% germination of spores after an 8-h dew treatment. This increased to more than 90% after a 24-h exposure to dew.

Clearly, there is a need to quantify and better understand the effectiveness of bioherbicides applied as foliar sprays since this type of application can be wasteful of the applied bioherbicide material, through drift, lack of spore retention in the droplet, and deposition on nontarget sites (Chapple et al., 1996; Greaves et al., 1998). Therefore, more 'intelligent' application systems should be tested and adopted for delivery of weed control pathogens. In this regard, innovations such as the dual nozzle sprayers (Chapple et al., 1996), use of compressed air rather than CO_2 propulsion, to minimize acidification of the spray mixture by the latter (Rosskopf et al., 1997), and sensor-controlled sprayers (Hanks and Beck, 1998), such as Detectspray™ (North America Pty. Ltd., Albury, NSW, Australia) and WeedSeeker™ (Patchen, Inc, A Subsidiary of Deere and Company, Los Gatos, CA, USA) housed in spray hoods, such as Redball® (Custom Ag Products, Benson, MN, USA), are worth exploring for the delivery of bioherbicides.

An exciting new development in the application of bioherbicides is a device called the Burch Wet Blade™ mower. This system consists of a riding mower that has a specially engineered mower assembly and a programmable fluid-delivery device. A controlled volume of a fluid (e.g., a bioherbicide suspension) is discharged on the mower blade, which, as a result of the centrifugal force generated during the high-speed spinning/cutting action

of the blade, is spread on the under side of the blade. As the vegetation is cut, the liquid containing the active ingredient (bioherbicide) is smeared on the cut surface and pulled into the cut shoots by capillarity. Using this device, DeValerio et al. (2000) have successfully demonstrated the control of *Solanum viarum* with the bacterial pathogen *Ralstonia solanacearum*. The wet-blade concept has significant implications as a delivery tool for bioherbicides as well as chemical herbicides. It is conceivable that robotic wet-blade mowers could be designed to control weeds between rows, thereby eliminating the need for cultivation. Since wastage due to nontarget deposition and drift of the bioherbicide product can be minimized to a very great extent, the wet-blade application may be used to improve the already excellent margin of safety of bioherbicides.

A few novel tools designed primarily to deliver chemical herbicides to weedy tree species could be adopted to deliver bioherbicides. For example, EZ-JECT™ Lance and EX-JECT™ capsules could be loaded with a bioherbicide preparation and forcibly implanted into stumps (both from Monsanto Chemical Co., St. Louis, MO, USA). GEL CAP™ Application Tool and GEL CAP™ cartridge containing a liquid formulation of a bioherbicide could be screwed onto a tree for gradual release of the bioherbicide (both from Pace Chemicals Ltd., Canada). PFC-ALDERWAK™ (Pacific Forestry Centre, Victoria, BC, Canada) was designed specifically to be used with *Nectria ditissima* to control *Alnus rubra* (Dorworth, 1995). However, these implements have not been widely used to deliver bioherbicides. For example, the bioherbicides developed for use against trees (BioChon and the soon-to-follow Chontrol, from MycoLogic Inc, Canada, and Stumpout) are applied as pastes or liquids over cut stumps.

Novel approaches

Three approaches are being tested to improve the spectrum of weeds controlled or to increase the level of control while improving consistency. The first is the attempt to use of a mixture of three pathogens to control several weeds. This approach, a ‘multiple-pathogen strategy’, has promise for further development (Chandramohan, 1999; Chandramohan et al., 2000). The second is the use of *Pseudomonas syringae* pv. *tagetis*, as a broad-spectrum pathogen with the aid of an organosilicone surfactant such as Silwet L-77 (Johnson et al., 1996). The third is the use of a wide-host-range pathogen such as *Sclerotinia sclerotiorum* in a host-restricted manner with the help of genetic and nutritional engineering (Sands et al., 1990).

A bioherbicide system based on three fungal pathogens, *Drechslera gigantea, Exserohilum longirostratum*, and *Exserohilum rostratum*, which were isolated respectively from *Digitaria sanguinalis, Dactyloctenium*

aegyptium, and *Sorghum halepense* in Florida, is undergoing development for use in citrus groves (Chandramohan, 1999; Chandramohan et al., 2000). In greenhouse trials, these pathogens, when used individually or as a cocktail containing a mixture of all three fungi (a total of 2×10^5 spores/ml in 1:1:1 v/v), caused severe foliar blighting and killed 4-week-old plants of *D. sanguinalis, D. aegyptium, Panicum maximum, S. halepense, Cenchrus echinatus, Panicum texanum*, and *Setaria glauca*. These fungi were nonpathogenic to many nontarget crop species, including citrus that were screened in a host-range study. These pathogens have been successfully field-tested using an emulsion-based inoculum preparation (40% oil concentration) of each pathogen as well as the pathogen mixture. The seven weedy grasses mentioned were controlled, each on average up to 85%, and the control lasted for 14 weeks without significant regrowth. Furthermore, emulsion-based inoculum preparations of the pathogens and the pathogen mixture effectively controlled a natural field population of *P. maximum* and the control lasted for at least 10 weeks without regrowth.

The bacterial pathogen *Pseudomonas syringae* pv. *tagetis* is the causal agent of a disease characterized by apical chlorosis on several members of Asteraceae. Johnson et al. (1996) have demonstrated that this bacterium can be used to control various weeds in and outside the Asteraceae family. Spray application of this bacterium, at 5×10^8 cells/ml, in an aqueous buffer containing the surfactants Silwet L-77 (0.1%) or Silwet 408 (0.2%) resulted in 100% disease incidence and a higher level of disease severity on *Cirsium arvense* than observed in natural infections. In addition to *C. arvense*, the following plants were severely diseased when sprayed with the bacterial cells: *Ambrosia artemisiifolia, Helianthus annuus, H. tuberosus*, and *Tagetes erecta*. Under field conditions, high levels of plant mortality (57–100%) were seen in the case of *A. artemisiifolia, C. arvense, Conyza canadensis, Lactuca serriola*, and *Xanthium strumarium*. In addition, severe injury was seen on infected *Setaria viridis* and *Abutilon theophrasti*. Symptoms appeared in some species within 3 to 4 days and populations of *A. artemisiifolia, C. canadensis, L. serriola*, and *X. strumarium* were virtually eliminated, while populations of *C. arvense* were significantly reduced compared to controls. Tissue formed before the bacterium was applied, such as mature leaves, was not affected. However, once apical chlorosis was induced, seed production appeared to be inhibited in the case of *C. arvense* (Johnson et al., 1996). Further research is in progress on this bioherbicide agent under the Cooperative Regional Research Project S-268, with Encore Technologies, Minnetonka, MN, as the commercial developer of this agent (unpublished reports of S-268, available from the author).

Sclerotinia sclerotiorum is a fungal pathogen that is reported to attack in excess of four hundred different plant species. It causes economically significant yield losses in several crops. Typically, infected plants are rapidly killed and the disease spreads to adjacent susceptible plants. Sands et al. (1990), have provided a rationale for the development and use of this widespread, host-unspecialized, plurivorus pathogen as a bioherbicide. They have argued that few plant pathogens are both lethal and sufficiently host-specific to be effective weed control agents. Indeed, highly host-specific organisms that coexist in a state of balanced parasitism seldom kill their hosts. Sands et al. (1990) and Bourdôt et al. (2000) have further reasoned that *S. sclerotiorum* can be used safely, with appropriate precautions, as a bioherbicide. Sands et al. (1990) have demonstrated that it is possible to genetically restrict the host range or to decrease the survival and/or spread of the pathogen through ultraviolet or chemical mutagenesis. They were able to produce four classes of mutants: auxotrophs that only attack plants when supplied with an exogenous source of a required nutrient, sclerotium-nonforming mutants, and reduced virulence or altered host-range mutants. Harvey et al. (1998) tested two auxotrophic mutants of *S. sclerotiorum* in greenhouse and field trials for pathogenicity to Canada thistle with and without amino acid amendments. Whereas an arginine auxotroph was pathogenic with or without arginine amendment, a leucine auxotroph was poorly pathogenic in the absence of leucine amendment and was generally less pathogenic than the wildtype or the arginine auxotroph. Two wildtype strains gave significant reductions in *C. arvense* cover within 3 months of treatment. The auxotrophic strains did not reduce weed cover in the season of treatment but reduced stem height and plant density in the following spring. The auxotrophic strains were less fit than the wildtype strains in promoting disease development in the field.

Miller et al. (1989) have produced a mutant of *S. sclerotiorum* lacking the ability to produce sclerotia. Conceivably, this mutant would not overwinter or easily spread, minimizing the possibility of damage to spring crops. However, it is not known if this mutant has been field-tested, but studies by Brosten and Sands (1986) and Hurrell et al. (2000) with wildtype strains have confirmed the feasibility of suppressing *C. arvense* populations under field conditions.

Targeting weeds of worldwide importance

Several new pathogens are undergoing testing and development for weeds of worldwide importance (Table 1). Examples of weeds in this category are *Amaranthus* spp., *Chenopodium* spp., *Cuscuta* spp., *Cyperus* spp., *Echinochloa* spp., *Eichhornia crassipes, Striga* spp., *Orobanche* spp., *Portulaca oleracea, Senna obtusifolia*, submerged aquatic weeds such as *Egeria* spp., *Hydrilla verticillata, Myriophyllum spicatum*, and *Potamogeton* spp.,

Taraxacum officinale, and various weedy grasses and invasive tree species. Given the market potential of these wide-spread weeds, it is hoped that there will be sufficient commercial interest in developing bioherbicides for at least a few of these weeds in the next decade.

Augmentation strategies

Theoretically, it is possible to increase the negative impacts of a native or naturalized pathogen on a weed population by maintaining an inoculum source (conservation) and promoting early inoculum dispersal to start new epidemics in the spring (augmentation). This approach could have applications in cropping systems that rely on low chemical inputs (e.g., organic farming) and minimal physical disturbance (e.g., conservation tillage). In order for this approach to be widely accepted, crop production and pest management systems should be developed to identify suitable pathogens and complementary tactics (e.g., crop row-spacing, conventional tillage, minimum tillage, no tillage, cover crops, and others) that could be integrated to manage a weed problem. By necessity, this approach would require research on a case-by-case basis to develop systems to match the particular weed problems (i.e., a system-management approach).

Müller-Schärer and Frantzen (1996), Frantzen and Hatcher (1997), Frantzen and Müller-Schärer (1998) and Frantzen et al. (this issue) have provided detailed analyses of the theory and practicability of the system-management approach to biological control of weeds. This approach may be well-suited to situations where it is necessary to control single weed species in crops and where immediate and complete control is not required, the production of large amounts of the agent is limiting due to the biotrophic nature of the pathogen, and/or the importation of an exotic agent is not possible. To practice this approach, it is necessary to develop an understanding of the infection window, the genetic structure of the plant and pathogen populations, and the management of the infection conditions to maximize the spread and impact of the disease on the weed, and to minimize the development of resistant weed populations. Joint application of herbicides at low rates, additional necrotrophic pathogens, and of biochemicals capable of interfering with the weed's defense reactions are also possible companion strategies to this approach.

To demonstrate the applicability of this approach, the rust fungus *Puccinia lagenophorae* was used to control the annual weed *Senecio vulgaris*. Although this host-pathogen system may be under some level of homeostasis in Europe, as evidenced by the presence of weed biotypes and pathogen races controlled by quantitative host resistance, the pathogen appears not to be constrained in its ability to reduce the weed's reproduction and compe-

titive ability (Wyss and Müller-Schärer, 1999). Furthermore, results of field studies at a ruderal site suggested that only a few weak sources of inoculum are needed to start a rust epidemic in *S. vulgaris* populations in the spring (Frantzen and Müller-Schärer, 1999).

The applicability of the system-management approach was tested in a small-scale field experiment with celeriac (root celery), intersown with an inbred line of *S. vulgaris*. The rust fungus *P. lagenophorae* was introduced into parts of the plot and its impact on the competitive balance between the crop and weed in the presence and absence of a herbicide treatment was studied. Competition from a density of 50 *S. vulgaris* plants/m^2 during the first 10 weeks of crop growth was substantial, resulting in a 28% reduction in the fresh weight of celeriac bulbs. The epidemic spread of the rust fungus was relatively fast, and the time to infection was similar to that in full-area applications. The fresh weight of the celeriac bulbs in plots with both *S. vulgaris* and the rust was equal to that of bulbs from weed-free plots. Thus, artificial stimulation of rust infection on *S. vulgaris* strongly reduced crop loss due to competition from the weed. The reduction in the observed yield loss was due to reduced biomass of *S. vulgaris* and not reduced survival of the weed. As an added benefit, infected but surviving *S. vulgaris* plants may contribute to soil cover and help to suppress later-germinating weed species (Müller-Schärer and Rieger, 1998).

A list of new research needs

In addition to the ongoing studies based on previously identified needs (Auld and Morin, 1995; Charudattan, 1991; Greaves et al., 1998; and others), future research in this field should consider weed targets and weed management needs that are most urgent and problematic for management by conventional control strategies. These represent opportunities where biological control agents can succeed with potentially significant benefits to the users.

1. Bioherbicides for herbicide-resistant weeds.
2. Identification and cloning of genes for virulence, host susceptibility, and host-parasite recognition – all using suitable weed-pathogen models.
3. Biological control agents for invasive weeds in natural areas. Although generally invasive weeds cause problems in natural, ruderal sites, they can spread to agricultural lands as well. Problems of invasive weeds are bound to become more serious on a global scale due to the ever-increasing degradation of land and water by the escalating human population and the consequent onslaught on the environment. It is unimaginable, both from economic and ecological standpoints, to think that invasive weeds can be managed by regulations (exclusion and quarantine) or

physical and chemical controls. Biological control, in all of its aspects, should be the centerpiece of a global strategy to tackle invasive weeds.

4. More studies on the system-management approach, taking into account not only the costs but also the benefits of weeds (Hurle, 1997). Some weed pathosystems suitable for exploitation are given in Table 1.
5. Studies on variability in weed biotypes and pathogen populations as a means to improve and predict the suitability of weed-pathogen systems selected for biological control.
6. More efforts to identify and utilize integrated systems consisting of insect and microbial biocontrol agents (e.g., pathogens and rhizobacteria; Table 1).

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