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Plant Pathogens at Work: Progress and Possibilities for Weed Biocontrol Classical versus Bioherbicidal Approach

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Weeds are a perpetual menace to agricultural productivity, causing significant reductions in the quantity and quality of crop yields. Weeds can reduce crop yields by an average of 12%, which translates to $32 billion in losses per year (43). Growers incur costs from herbicide use, employment of tillage and mowing, and cultural and biological inputs for weed management. In 2001, approximately $6.4 billion were spent in the United States on herbicides, which represents 58% of the total pesticide expenditures in the country (23).

Weeds pose serious ecological problems; invasive weeds in natural areas alter ecosystem processes and displace native plant and animal species. They may also support populations of non-native animals and microbes and hybridize with native species, subsequently altering gene pools (33). Babbitt (1) estimated that non-native weed species are spreading and invading United States wildlife habitat at the rate of 700,000 ha annually. These non-native weeds include the European purple loosestrife (*Lythrum salicaria*) (39), the European cheatgrass (*Bromus tectorum*) (45), and the Australian melaleuca (*Melaleuca quinquenervia*) (Fig. 1) (12).

Fig. 1. Typical monoculture of Australian melaleuca (*Meleleuca quinquenervia)* trees in Florida prior to control efforts. Photo courtesy of Min Rayamajhi.

Numerous challenges for researchers, growers, and land managers have resulted from: the negative effects of existing weed control practices; loss of herbicide registrations; the ban on methyl bromide; lack of herbicides for minor crops, non-agricultural weeds and non-native invasive weeds; the cost of control methods in natural areas; and the need for control methods that are appropriate for use in organic production systems. These challenges create niches where the use of plant pathogens as biological control agents for weeds could be a viable alternative.

Biological control is a selective process in which a pathogen or an insect is used against targeted weeds without damaging non-target plant species (20). The use of plant pathogens to suppress weeds is an alternative weed control option for areas or systems where the use of chemical herbicides is not permitted or feasible or where production practices lead to uncontrolled weed monocultures (Fig. 2). However, biological weed control agents are utilized to mitigate weed infestations and not to eradicate entire weed populations. The inability of these agents to damage weeds as severely as chemical herbicides has deterred the commercialization of many biological control agents. Biological control will be most effective when the strategy employed is tailored to the specific weed management needs of the situation.

Fig. 2. Virtual weed monoculture of purple nutsedge (*Cyperus rotundus*) in a squash production system that utilizes polyethylene mulch for fumigant retention and weed management.

Weed biocontrol with plant pathogens has been studied using two basic approaches: the classical and the bioherbicide approaches.

Classical Approach

The biocontrol approach using an imported pathogen to control a native or naturalized weed with minimal manipulations has been termed the classical or inoculative biocontrol method. Introduced weeds, especially those that are clonally reproducing, genetically homogeneous, and reproductively conserved, can be easy targets for control by the introduction of coevolved pathogens from which they have been physically separated for a period of time. In classical biocontrol programs, the introduced pathogen is released or inoculated into small weed infestations relative to the total infestation. If conditions are favorable, the pathogen multiplies and spreads, causing an epidemic that may kill or severely limit the growth and reproduction of the weed. Since the disease increase will typically be gradual rather than instantaneous, months or years may pass before a significant level of weed control is seen.

Two caveats concerning the classical approach: it is impossible to predict the success of an introduced pathogen, and it is not realistic to be prepared for a total recall should a released agent be subsequently deemed undesirable. Therefore, a careful evaluation of efficacy and safety precedes a pathogen's introduction. Valid protocols based on conceptual frameworks as well as empirical examples exist for selection of safe and effective agents (6,16). As Barton (3) found in an extensive analysis of projects during the past several decades, the safety record of worldwide pathogen introductions for weed control has been impeccable with not a single instance of unexpected, undesirable effects.

The overall success rate of classical weed biocontrol projects using imported pathogens has been estimated at 57% and for all pathogen-based weed control projects is 21%. These success rates are calculated from the number of projects for which success can be verified from published accounts or reliable anecdotes compared to the number of known projects (15). The record of success for insect-based weed biocontrol projects, at around 30 to 35% (see discussion in 15), is comparable. Given the potential for additive or synergistic effects of different pathogens as well as the possible beneficial interactions between pathogens and insects, it would be prudent to consider the integration of pathogens and insects in future weed control projects (11). Since the early 1970s, seven pathogens have been imported into the United States: *Puccinia chondrillina*, *P. carduorum*, and *P. jaceae* (all in the mainland); and *Entyloma ageratinae* (also described as *E. compositarum*), *Colletotrichum gloeosporioides* f.sp. *clidemiae*, *Septoria passiflorae*, and a *Septoria* sp. on lantana (all in Hawaii). Worldwide, this number is 25 (3).

Generally, pathogens intended as classical biocontrol agents are subjected to rigorous safety and host-specificity testing under the oversight of the Technical Advisory Group (TAG) on Biological Control of Weeds. TAG is a voluntary

committee under the aegis of the USDA's Animal and Plant Health Inspection Service, Plant Protection and Quarantine (APHIS-PPQ) (17,24,28). TAG plays an oversight role in reviewing proposals to initiate classical weed biocontrol projects and in making recommendations with respect to the need, scope, and adequacy of the proposed research. Based on TAG's recommendation, APHIS-PPQ grants permits to introduce foreign pathogens into approved quarantine facilities as well as their eventual release and field establishment. Prospective pathogens are studied in their native range to determine their host specificity and virulence towards the target weeds. Those considered safe to non-target plants are reviewed by TAG and approved by APHIS-PPQ for introduction. Once in quarantine, additional testing is done on plants of economic and ecological importance to North America.

The importance of precise identification of the pathogen and confirmation of its virulence toward the target genotype is important because the host-pathogen specificity can be governed by single-gene differences or by a small number of genes, particularly at the subspecies level. A poor understanding of the taxonomy of the weed target, plant pathogen, or the underlying host-pathogen relationship can cause delays or a permanent halt to the biocontrol project due to the agent's unsatisfactory performance in assessment studies.

Formal attempts at classical biocontrol of weeds began in the late 1960s with a project to find and use pathogens for *Rumex* spp. in the United States (22) and blackberries (*Rubus* spp.) in Chile (32). Since the 1970s, there have been several highly successful classical biocontrol programs [for reviews see (4,15,44)].

Among the most successful is the control of *Acacia saligna* by *Uromycladium tepperianum* introduced into South Africa from Australia (31). *Acacia saligna* is regarded as the most important invasive weed threatening the Cape Fynbos Floristic Region of South Africa, a unique ecosystem. The fungus causes extensive gall formation causing heavily colonized branches to droop; the tree is eventually killed. The fungus was introduced into the Western Cape province between 1987 and 1989. In about eight years, the disease had become widespread and tree density was decreased by 90 to 95%. The number of seeds in the soil seed bank had also stabilized in most sites and the process of tree decline was continuing (30).

Another widely acclaimed example is the use of *Puccinia chondrillina* to control *Chondrilla juncea* (rush skeleton) in Australia (18). *Puccinia chondrillina* was also introduced into the western United States to control a skeletonweed biotype. However, unlike in Australia, the rust was only partially successful. The rust has been utilized with chemical herbicides, and the insect biocontrol agents, *Cystiphora schmidti* (a gall forming midge) and *Aceria chondrillinae* (a gall forming mite), in an integrated management program (26). As in Australia, the rust has still been the most successful of the three introduced biocontrol agents in California and other western states (36).

Another successful weed biocontrol program uses the foliar smut fungus, *Entyloma ageratinae* from Jamaica, to control Hamakua pamakani (*Ageratina riparia*) in Hawaii (41) (Fig. 3). The fungus, originally misnamed as *Cercosporella* sp. and subsequently described as *Entyloma ageratinae* by Barreto and Evans (2) and *E. compositarum* by Trujillo et al. (41), was introduced into Hawaii in 1974. A few months after the field release, devastating epidemics were recorded in dense stands of *A. riparia* in cool, high-rainfall sites in Oahu, Hawaii, and Maui, causing significant stand reductions within 9 months. Similar reductions in weed populations were recorded 3 to 4 years after the pathogen was released at sites with adequate moisture. At sites with low temperatures and low rainfall there was greater than 50% reduction in the weed population in 8 years after the pathogen's release. It is estimated that more than 50,000 ha of pasture land have been rehabilitated to their full potential due to this pathogen. No evidence of host resistance or the presence of mutant strains of the pathogen has been encountered (40,42). This pathogen has also been released against *A. riparia* in South Africa (29) and New Zealand (19), where it is showing signs of success (21,29).

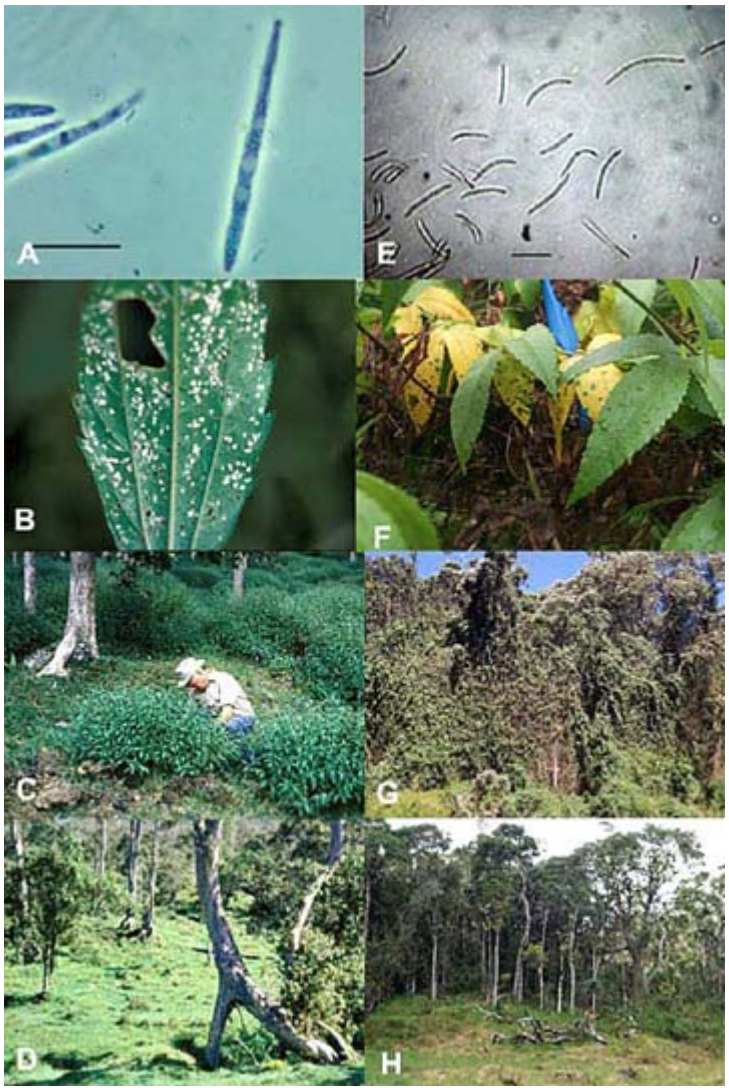

Fig. 3. Biological control of Hamakua 'Pa-makani,' *Ageratina riparia*, with *Entyloma compositarum*, the white smut fungus introduced from Jamaica in 1974. (**A**) Nonseptate, hyaline, slender, arcuate conidia (30-40 x 3-3.5 µm) of*E. compositarum*. Scale bar = 12 µm. (**B**) Abaxial surface of a diseased 'Pa-makani' leaf showing the characteristic white sporodochia, containing masses of spores of *E. compositarum*. (**C**) Infestation of *A. riparia* at 900 m elevation at Palani ranch, North Kona, Hawaii, before inoculations in December 1975. (**D**) Striking biological control of the 'Pa-makani' weed at Palani ranch, a site at 900 m elevation, 8 years after inoculation with the biocontrol fungus. (E-H) Biological control of banana poka *Passiflora tarminiana* with *Septoria passiflorae* introduced from Ipiales, Colombia in 1993. (**E**) Filiform, multiseptate, hyaline conidia of S. passiflorae (35-52 × 1.5-2 µm). Scale bar = 24 lm. (**F**) Symptoms of septoria leaf spot on banana poka leaves 30 days after inoculations with 'lei inoculum.' Notice necrotic dry leaves, remains of the original lei that was placed below the symptomatic leaves. (**G**) Piha-road bordering the US Department of the Interior-Fish and Wildlife Preserve Photopoint No. 2, 1850 m elevation, before the 1997 inoculation with *S. passiflorae*. Notice the banana poka vine climbing to the top of the koa forest. (**H**) Photopoint No. 2 showing 99% banana poka biomass reduction 6 years after inoculation. Reprinted from Biological Control, Volume 33, Issue 1, Eduardo E. Trujillo, History and success of plant pathogens for biological control of introduced weeds in Hawaii, pp. 113-122, Figure 2, 2005, with permission from Elsevier. Use of (G) and (H) by permission of the American Phytopathological Society. Reprinted from Biological Control, Volume 33, Issue 1, Eduardo E. Trujillo, History and success of plant pathogens for biological control of introduced weeds in Hawaii, pp. 113-122, Figure 2, 2005, with permission from Elsevier.

A more recent example is that of *Puccinia carduorum*, imported from Turkey and released into the northeastern United States in 1987 to control musk thistle, *Carduus thoermeri*. The rust has spread widely from its original introduction to the western states of Wyoming and California (5,10,27). *Puccinia carduorum* has been found to reduce musk thistle density by accelerating senescence of rust-infected musk thistle and reducing seed production by 20 to 57% (5). The effects of this fungus on insect biocontrol agents of this weed are negligible (25).

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*). Another introduction into Australia that appears to be producing successful results is *Sphaerulina mimosae-pigrae* on *Mimosa pigra*. The most recent introduction to the United States, *Puccinia jaceae* var. *solstitialis* imported from Bulgaria and Turkey, was released in California in 2003 (Figs. 4 and 5). The host range tests on this pathogen were extensive (8,9) and the effects of this introduction are being monitored.

Fig. 4. Infestation of yellow starthistle (*Centaurea solstitialis*) in California. The weed is the target of the classical biological control agent, *Puccinia jaceae* var. *solstitialis*. The host range of the rust was studied extensively prior to its release in California in 2003. The impact and movement of the fungus is currently being monitored (Bill Bruckart, *personal communication*). Photo courtesy of Bill Bruckart.

Fig. 5. (A) Initial field infection of yellow starthistle leaf in Tehama Co., California, by the biocontrol agent, *Puccinia jaceae* var. *solstitialis* (Photo by Baldo Villegas, CDFA) and (B) prolific greenhouse production of urediniospores (Photo by Bill Bruckart). Photos courtesy of Bill Bruckart.

Bioherbicide Approach

The bioherbicide approach utilizes indigenous plant pathogens that are isolated from weeds and are cultured to produce large numbers of infective propagules. These are applied at rates that will cause high levels of infection, leading to suppression of the target weed before economic losses are incurred (38). Annual applications are required since the pathogen does not generally survive in sufficient numbers between growing seasons (13,35,37).

There are more than 200 plant pathogens that have been evaluated for their potential as bioherbicides; these include fungi and bacteria that cause foliar diseases, soil-borne fungal and bacterial pathogens, and deleterious rhizobacteria (DRB) (7,14,34). However, there are few that have been registered and are commercially available. According to Barton (4), from the 1960s to 2005, numerous bioherbicidal plant pathogens have been registered, including the following: in the United States, *Acremonium diospyri*, *Phytophthora palmivora* [DeVine], *Colletotrichum gloeosporioides* f. sp. *aeschynomene* [Collego], *Alternaria cassiae* [CASSTTM], *Puccinia canaliculata* [Dr. BioSedge], *P. thlaspeos* [Woad Warrior], *Chondrostereum purpureum* [Myco–TechTM Paste and ControlTM Paste], and *Alternaria destruens* [Smolder]; in Canada, *C. gloeosporioides* f. sp. *malva*e [BioMal], *Chondrostereum purpureum* [Myco–TechTM paste and ControlTM/EcoclearTM]; in China, *C. gloeosporiodes* f. sp. *cuscutae* [Lubao]; in South Africa, *Cylindrobasidium leave* [Stumpout] and *C. gloeosporioides* [Hakatak]; in the Netherlands, *C. purpureum* [BiochonTM]; and in Japan, *Xanthomonas campestris* pv. *poae* [CampericoTM]. One bioherbicide agent, *C. gloeosporioides* f.sp. *aeschynomene* (previously Collego), has been re-registered under the commercial name LockDown for use in rice in Arkansas, Louisiana, and Mississippi (David O. TeBeest, *personal communication*).

The ability of a pathogen to cause damage on its target weed is influenced by many factors and interactions, such as inoculum concentration and application rate, environmental conditions, formulation, spray parameters, target weed age or growth stage, other micro and macroorganisms, and other pesticides. Numerous studies have been done to find ways to improve efficacy and achieve acceptable levels of weed control in conventional, non-conventional and natural systems.

Weed biological control using plant pathogens has been successfully implemented for a number of important invasive weeds. Both the classical and bioherbicide approaches have shown promise depending on the characteristics of the target weed. Bioherbicidal activity can be improved with research on formulation and application technology. Other approaches that have improved weed control efficacy for both classical biological control agents and bioherbicides include using a combination of pathogens and insects.

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