

BIOHERBICIDES: RESEARCH AND RISKS

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*Many microbes have bioherbicidal activity, and several phytopathogenic fungi and bacteria have been patented as weed-control agents. The phytotoxic components of most agents have not been elucidated, but some phytotoxins and other secondary compounds produced by such microbes may be toxic to mammalian systems. Furthermore, few rigorous assessments have addressed uptake, translocation, metabolism, and persistence of these phytotoxins (some of which have not been identified), or the environmental effects of repeated augmentative applications of these microorganisms on long-term impact, environmental fate, or interactions with other microbial communities. Generally, there is a lack of definitive research on the overall toxicological risk of bioherbicidal microorganisms to the degree achieved or required for synthetic herbicides. This article presents a brief overview of bioherbicides (microorganisms and/or their phytotoxins), with emphasis on the toxicity of certain bioherbicides, and general considerations of risks associated with bioherbicidal use. A subsequent article presents some of our research results and future research directions on efforts to develop the bioherbicidal fungus *Myrothecium verrucaria* as a safe and efficacious bioherbicide have been published elsewhere.*

Keywords: Bioherbicide, phytotoxin, microbial weed control, mycotoxin regulation, natural product toxicology, phytopathogen, secondary products, trichothecene biosynthesis

Introduction

Bioherbicides include phytopathogenic microorganisms or microbial compounds useful for weed control. Collectively these organisms and/or their natural products are called bioherbicides.

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Fungi with potential bioherbicidal activity are also termed mycoherbicides. Bioherbicide propagules are applied augmentatively at high densities (inundative) onto weeds, and like herbicides, bioherbicides require application at each cropping season. Since many of these bioherbicidal microbes (especially fungi) have little or no potential to propagate to epidemic levels after application, reapplication of the same organism is required each growing season to achieve adequate weed control. This use of pathogens for inundative bioherbicidal weed control differs from "classical biological control," where organisms are released and allowed to spread to host plants via natural dispersion in the environment.

The initiative for using pathogens, phytotoxins from pathogens, and other microorganisms as biological weed-control agents began about three decades ago. Since then, numerous microbes have been screened for phytotoxic potential, and several dozens evaluated as bioherbicides as reported by various researchers and summarized (e.g., Hoagland, 1990, 2001; TeBeest, 1991). Due to the interest in this area, many other weed pathogens and phytotoxins (from pathogenic and nonpathogenic microorganisms) will be discovered that possess bioherbicidal activity. Most bioherbicides have been targeted toward agronomic weeds, but these agents may also be useful to control weeds in nonagronomic areas (recreational areas, forests, rights-of-way, lawns, gardens, etc.) where synthetic herbicides are not registered, or where their use is cost-prohibitive.

Bioherbicidal phytopathogens also have potential for use in integrated weed management programs, if the organisms can tolerate various agricultural chemicals. Genetic engineering and microbial strain selection might also be used to increase pathogen virulence, alter host range, and enhance interactions with other chemical regulators or synergists. Many fungi have potential as mycoherbicides (Table 1).

Other fungi have been shown to have broad-spectrum weed control ranges (Table 2). Only a very few organisms have been patented for use as weed-control agents and several bioherbicides have achieved commercial status and have met registration requirements (Table 3). Even though these organisms are effective weed-control agents, little research on the risks of these microbes on nontarget plants, animals, and microbial communities or on

TABLE 1 Examples of Fungal Bioherbicides for Economically Important Terrestrial and Aquatic Weeds*

Weed	Pathogen	Reference
Velvetleaf	<i>Colletotrichum coccodes</i> <i>Fusarium lateritium</i>	Hodgson et al., 1988 Walker, 1981
Giant ragweed	<i>Fusarium lateritium</i>	Anonymous, 1989
Wild oat	<i>Septoria tritici</i> Desm. F. Sp. <i>Avenae</i>	Madariaga and Scharen, 1985
Common lambsquarters	<i>Ascochyta caulina</i> <i>Cercospora chenopodii</i> <i>C. dubia</i>	Scheepens and van Zon, 1982 Scheepens and van Zon, 1982 Scheepens and van Zon, 1982
Field bindweed	<i>Phomopsis convolvulus</i>	Anonymous, 1989; Vogelgsang et al., 1998
Yellow nutsedge	<i>Cercospora caricis</i>	Anonymous, 1989
Purple nutsedge	<i>Phyllachora cyperi</i>	Anonymous, 1989
Large crabgrass	<i>Pyricularia</i>	Anonymous, 1989
Barnyardgrass	<i>Cochliobolus lunatus</i>	Scheepens, 1987
Water hyacinth	<i>Alternaria eichhorniae</i>	Shabana, 1987
Goosegrass	<i>Bipolaris setariae</i>	Anonymous, 1989
Common purslane	<i>Dichotomophthora indica</i> <i>D. portulacae</i>	Evans and Ellison, 1988 Evans and Ellison, 1988
Itchgrass	<i>Curvularia</i> sp. <i>Phaeoseptoria</i> sp.	
Johnsongrass	<i>Sphacelotheca holci</i> <i>Bipolaris halepense</i> <i>B. sorghicola</i> <i>Colletotrichum graminicola</i> <i>Gloeocercospora sorghi</i>	Massion and Lindow, 1986 Chiang et al., 1989 Winder and Van Dyke, 1989 Anonymous, 1989 Anonymous, 1989
Sicklepod	<i>Pseudocercospora nigricans</i>	Hofmeister and Charudattan, 1987

*Modified from Charudattan 1990.

soil and water quality has been published. Overall, a few major points are evident. In many cases, bioherbicidal activity has been demonstrated for a pathogen or for a crude microbial extract, but generally the phytotoxic compounds and mechanism(s) involved remain unresolved. Most microorganisms with bioherbicidal potential have not been examined for their phytotoxic modes of action, that is, digestive enzymes, identity of specific phytotoxins, the possibility of multiple phytotoxins, and other virulence factors. Furthermore, the toxicity of specific phytotoxins to nontarget organisms has only rarely been investigated and most

TABLE 2 Examples of Broad-Spectrum Fungal Bioherbicides Tested for Weed Control*

Pathogen	Weed species or family	Reference
<i>Alternaria cassiae</i>	Sicklepod Coffee senna Showy croton	Boyette, 1988; Charudattan et al., 1986; Walker, 1982, 1983
<i>Amphobotrys ricini</i>	Members of Euphorbiaceae	Holcomb et al., 1989; Whitney and Taber, 1986
<i>Colletotrichum gloeosporioides</i> various f. spp.	Members of Leguminosae, Malvaceae, Convolvulaceae (dodders)	Daniel et al., 1973; Mortensen and Makowski, 1997
<i>C. dematium</i>	Members of Leguminosae	Cardina et al., 1988
<i>C. graminicola</i>	Members of Gramineae	Anonymous, 1989
<i>Exserohilum monoceras</i>	<i>Echinochloa</i> spp.; itchgrass	Zhang and Watson, 1997
<i>Fusarium lateritium</i>	Velvetleaf Giant ragweed Spurred anoda Prickly sida <i>Potamogeton</i> spp.	Walker, 1981 Anonymous, 1989 Walker, 1981 Walker, 1981 Bernhardt and Duniway, 1986
<i>Myrothecium verrucaria</i>	Sicklepod; various species of other plant families	Walker and Tilley, 1997
<i>Pyricularia grisea</i>	Large crabgrass/ Goosegrass	Anonymous, 1989 Figliola et al., 1988
<i>Sclerotinia sclerotiorum</i>	Multiple genera and species	Brosten and Sands, 1986

*Modified from Charudattan 1990.

of these microbes have not been examined for potentially harmful effects or the production of other harmful chemicals. Mass-production of bioherbicides, and their distribution and use on a wide agricultural scale, could pose a significant exposure to man, animals, and the environment. Laboratory and field research of bioherbicides could also result in potential elevated exposure of researchers to these microbes and their secondary chemical products, if proper precautions are not exercised. Increased use of these products will raise the potential for adverse and unexpected health or environmental outcomes. These risks should be met with a concomitant increase of studies to assess potential hazards during product development, large-scale production, and release.

TABLE 3 Commercially Registered Bioherbicides

Pathogen	Weed host	Trade name	Reference
<i>Colletotrichum gloeosporioides</i> f. sp. <i>aeschynmene</i>	Northern jointvetch	Collego®	Bowers, 1986; Smith, 1982, 1991
<i>Colletotrichum gloeosporioides</i> f. sp. <i>malvae</i>	Round-leaved mallow	BioMal®	Boyetchko, 1999; Mortensen, 1998; Mortensen and Makowski, 1997
<i>Colletotrichum gloeosporioides</i>	Silky wattle	Hakatak™	Morris et al., 1999
<i>Phytophthora palmivora</i>	Stranglervine	DeVine®	Ridings, 1986
<i>Cercospora rodmanii</i>	Water hyacinth	ABG-5003	Charudattan, 1991, 2001
<i>Alternaria cassiae</i>	Sicklepod, coffee senna, and showy crotalaria	CASST™	Charudattan et al., 1986
<i>Alternaria</i> sp.	Dodder	Smolder®	Bewick et al., 2000
<i>Puccinia canaliculata</i>	Yellow nutsedge	Dr. BioSedge®	Bruckart and Dowler, 1986; Phatak, 1992
<i>Colletotrichum gloeosporioides</i>	Dodder	LuBao	Templeton, 1992
<i>Chondrostereum purpureum</i>	Black cherry	BioChon™ Stumpout®	Dumas et al., 1997 Shamoun and Hintz, 1998
<i>Cylindrobasidium leave</i>	<i>Acacia</i> spp.	ECOClear™	Butt, 2000
<i>Fusarium</i> spp.	Velvetleaf	Velgo®	Butt, 2000
<i>Xanthomonas campestris</i>	Annual bluegrass	Camperico®	Imaizumi et al., 1997

Phytopathogenic Fungi and Bacteria and Their Phytotoxins

Plant pathogens produce a variety of phytotoxins that interfere with plant metabolism, ranging from subtle effects on gene expression to plant mortality (Walton, 1996). The mode of action of a phytotoxin can be direct interaction with a specific plant component (e.g., enzyme or membrane receptor), but if that component is absent or altered, there is no phytotoxic effect. Thus phytotoxins and/or their molecular targets are important determinants of pathogen host range. Phytotoxins can be

TABLE 4 Examples of Host-Specific Toxins Produced by Phytopathogenic fungi*

Fungus	Toxin	Host and toxin properties
<i>Cochliobolus victoria</i>	HV-toxin	Specific for oats; pathogenicity determinant; induces cell leakage
<i>C. carbonum</i>	HC-toxin	Specific for maize; targets include plasma membrane
<i>C. nicotianae</i>	Colletotrichin	Toxic to tobacco
<i>C. heterostrophus</i>	T-toxin	Toxic to maize; mitochondria become leaky
<i>Alternaria alternata</i> <i>f. sp. lycopersici</i>	AAL-toxin	Disrupts pyrimidine synthesis in tomato (carbamoyl transferase inhibition); structural similarity to fumonisin B1 suggests ceramide synthase inhibition
<i>A. alternata</i> f. sp. <i>fragariae</i>	AF-toxin	Toxic to strawberry
<i>A. alternata</i> f. sp. <i>mali</i>	AM-toxin	Induces necrotic spots on apple leaves & fruit
<i>A. alternata</i> f. sp. <i>kikuchiana</i>	AK-toxin	Necrosis of Japanese pear
<i>A. alternata</i> f. sp. <i>terreus</i>	Acetylaranotin	Plant growth inhibitor
<i>A. alternata</i> f. sp. <i>citri</i>	ACTG-toxin	Toxic to mandarin orange

*Modified from Hoagland, 1990 and Yoder and Turgeon, 1985.

classified as nonspecific or host-specific. None of the nonspecific phytotoxins produced by pathogenic fungi have been rigorously evaluated for their precise roles in plant disease, but several host-specific phytotoxins have been studied in depth (Table 4). Some of these compounds are discussed below, although little information is publicly available on the production and properties of phytotoxins from commercialized bioherbicides.

Host-Specific Phytotoxins

Host-specific phytotoxins significantly affect only the plant species upon which the producing microorganism is pathogenic. Some host-specific phytotoxins are only toxic to certain cultivars of the host plant species. For example, *Alternaria alternata* f. sp. *lycopersici* is pathogenic to certain tomato cultivars, but recessive *asc/asc* genotypes are resistant (Abbas, Tanaka et al., 1995).

AAL-toxin causes injury to susceptible tomato cultivars, but does not affect resistant cultivars. Thus far, all known host-specific phytotoxins are derived from fungal pathogens. Only about twenty host-specific phytotoxins that affect crops have been reported (Scheffer and Livingston, 1984). AAL-toxin, thought to be a host-specific phytotoxin affecting crops, was found to be non-host-specific due to its phytotoxicity to a wide range of weed species (Abbas, Vesonder et al., 1992; Abbas, Vesonder et al., 1993; Tanaka et al., 1993). Destruxin B (discussed below) was also reported to be host-specific (Bains and Tewari, 1987), but was later found to be non-host-specific (Buchwaldt and Green, 1992).

Nonspecific Phytotoxins

These compounds are produced by both specialist and generalist plant pathogens. In the case of *Alternaria alternata* f. sp. *citri* (casual agent of brown spot disease of tangerines and mandarins), host-specific and nonspecific phytotoxins (e.g., tentoxin and tenuazonic acid) are produced in broth culture (Kono et al., 1986). The genus *Fusarium* includes plant pathogens, insect pathogens, and fungal biocontrol species (Desjardins, 1992; Teeter-Barsch and Roberts, 1983). One strain has been commercialized as a plant growth promoter via its ability to displace phytopathogenic *Fusarium* strains (Butt et al., 2001: 1–8). Another strain has potential to control the weed gorse (Morin et al., 2000). Phytopathogenic *Fusarium* species produce various chemical contaminants of plant tissues, including trichothecenes, fumonisins, naphthazarins, fusaric acid, and related pyridine derivatives (Desjardins, 1992). These compounds have varying degrees of phytotoxicity and toxicity to mammals. The phytotoxic aspects of *Fusarium* spp. and some of their products have been reviewed (Hoagland and Abbas 1995). The exact role of many of these compounds remains unclear, but some are also insecticidal (Grove and Pople, 1980). Other selected nonspecific phytotoxins are summarized in Table 5.

Bacterial Compounds

Bacteria also cause a multitude of diseases in crop plants and weeds. Since the discovery of tabtoxin (produced by *Pseudomonas syringae* var. *tabaci*), the causal agent of wildfire disease in

TABLE 5 Selected Examples of Microbial Non-Host-Selective Phytotoxins*

Source	Phytotoxin	Effect	Reference
<i>Alternaria carthami</i>	Brefeldin A	Chlorosis	Tietjen et al., 1983
<i>Alternaria helianthi</i>	Radicinin	Necrosis	Tal et al., 1985
<i>Alternaria macrospora</i>	Dehydrocurvularin	Necrosis	Robeson and Strobel, 1985
<i>Aspergillus terreus</i>	Acetylaranotin	Growth inhibition	Kamata et al., 1983
<i>Gladiolium virens</i>	Viridiol	Necrosis	Howell and Stipanovic, 1984
<i>Helminthosporium oryzae</i>	Ophiolbolin	Membrane disruptor	Cocucci et al., 1983
<i>Streptomyces griseus</i>	Naramycin B	Growth inhibition	Berg et al., 1982
<i>Streptomyces sp.</i>	Gougerotin	Growth inhibition	Murao and Hayashi, 1983
<i>Streptomyces viridochromogenes</i> , <i>S. hygroscopicus</i>	Phosphinothricin	Chlorosis, wilting, necrosis	Hoagland, 1999

*Modified from Hoagland, 2000.

tobacco (Steward, 1971; Taylor et al., 1972), other important bacterial phytotoxins have been discovered in *Pseudomonas* species (Table 6). Phaseolotoxin (from *P. syringae* pv. *Phaseolicola*) and coronatin (from *P. syringae* pv. *atropurpurea*) are both non-host-specific compounds, but coronatin's mode of action is not fully elucidated (Willis et al., 1991), and phaseolotoxin disrupts arginine metabolism via inhibition of ornithine carbamoyl transferase (Mitchell, 1976; Moore et al., 1984). Another bacterial bioherbicide, *Xanthomonas campestris*, has been registered to control annual bluegrass (see Table 3) (Imaizumi et al., 1997). A *Pseudomonas syringae* isolate has been registered to control Canada thistle (Johnson et al., 1996). Other *Pseudomonas syringae* phytotoxins include: coronatine, syringomycin, syringopeptin, tabtoxin, phaseolotoxin, and tagetetoxin (Table 6). *Pseudomonas syringae* pv. *syringae* produces syringomycin, syringotoxin, and syringostatin (Gross, 1991) and a new syringopeptin (Grugurina et al., 2002). *Pseudomonas syringae* pv. *coronafaciens* produces tabtoxin (Volksch and Weingart, 1998). Coronatine toxin (polyketide) is produced by *Pseudomonas syringae* pv. *tomato*.

With regard to risks of bacterial bioherbicides, closely related bacteria may or may not produce phytotoxins or possess phytopathological or human pathological or toxicological properties. For example, *Burkholderia (Pseudomonas) cepecia*, the causal agent

TABLE 6 Selected Phytotoxins Produced by *Pseudomonas* spp.*

Toxin	Mode of action	Reference
Cornatine	Methyl jasmonate mimic	Grant et al., 1990
Phaseolotoxin	Ornithine carbamyl transferase inhibitor	Gilchrist, 1983
Syngomycin	Plasma membrane disruptor	Ballio et al., 1991
Syngopeptin	Plasma membrane disruptor	Ballio et al., 1991
Tabtoxin	Glutamine synthetase inhibitor	Anzai et al., 1989
Tagetitoxin	Chloroplast RNA polymerase inhibitor	Steinberg et al., 1990

*Modified from Bender et al., 1999.

of bacterial rot in onions (Burkholder, 1950), has been developed as a biopesticide to protect crops plants against fungal diseases; a plant growth-promoting rhizobacterium; and a bioremediation agent for recalcitrant herbicide metabolism (King and Parke, 1996; McLoughlin et al., 1992; Reddy, 1997). However, over the past 20 years, *Burkholderia cepecia* has surfaced as a human pathogen (Holmes et al., 1998). Due to taxonomic problems, widespread distribution, and the phenotypic and genotypic complexity of these strains, their intentional agriculture use is highly cautioned (Holmes et al., 1998).

Examples of Toxic Compounds Produced (or Possibly Produced) by Photopathogenic Fungal Bioherbicides

Many secondary metabolites have been isolated and characterized from a large array of bacterial and fungal phytopathogens by numerous laboratories. Due to space constraints, we have selected fungal species (*Alternaria*, *Colletotrichum*, and *Fusarium*) that have been studied in major projects in our laboratory to exemplify metabolites that have either been implicated as phytotoxins and/or that exhibit mammalian toxicity. Similar compounds have also been selected from bacterial species.

Selected Fungal Metabolites

ALTERNARIA SPECIES

Mycotoxins from *Alternaria*, and specifically by *A. alternata*, are numerous. Among the most widely studied are tenuazonic

acid, alternariol, alternariol mono-methyl ether, altenuene, altertoxin I, and tentoxin (Griffin and Chu, 1983; Orved et al., 1988). Some of these compounds and others are presented below.

AAL-Toxin. AAL-toxin, a hydroxylated long-chain alkylamine containing a tricarboxylic acid moiety, is structurally related to the fumonisins (see below). It is produced by *Alternaria alternata* f. sp. *lycopersici*. In susceptible varieties of tomatoes, it caused rapid wilting and necrosis (Abbas, Tanaka et al., 1995). Its physiological effects in plant tissues appear to be identical to those of the fumonisins, and thus AAL-toxin is suspect for mammalian toxicity. Another *A. alternata* isolate has bioherbicidal potential to control water hyacinth and some other aquatic weeds (Babu et al., 2003), but there are no apparent reports concerning AAL-toxin production in this strain.

Alternariol. Alternariol and alternariol methyl ether were both shown to be nonmutagenic to strains TA98 and TA100 (with and without metabolic activation) in the Ames test. Other investigators indicated that alternariol methyl ether was weakly mutagenic to TA98 without metabolic activation, which may have resulted from the presence of low amounts of one of the highly mutagenic altertoxins in the alternariol methyl ether preparations (Davis and Stack, 2001).

Destruxins. The destruxins, produced by *Alternaria brassicae* and *Metarhizium anisopliae* (Buchwaldt and Green, 1992; Buchwaldt and Jensen, 1991), possess phytotoxicity toward a much larger range of susceptible plant species than the pathogens producing these compounds. Destruxin B causes necrotic and chlorotic symptoms in susceptible species (Buchwaldt and Green, 1992). Destruxin B, homodestruxin B, and desmethyl destruxin B are also produced by several other phytopathogenic fungi, such as *Alternaria brassicae*, *Trichothecium roseum*, and *Ophiosphaerella herpotricha* (Ayer and Pena-Rodriguez, 1987; Bains and Tewari, 1987; Buchwaldt and Jensen, 1991; Gupta et al., 1989). Other studies (Buchwaldt and Green, 1992) indicated that although destruxin B is mainly directed against *Brassica* species, other crucifers are also injured. Contrary to the non-host-specific reports, destruxin B from *Ophiosphaerella herpotricha* did not induce

phytotoxic reactions in Bermuda grass and other weeds, suggesting host-specificity (Venkatasubbaiah et al., 1994).

Little is known about the functionally active groups in the different destruxin molecules. It has been suggested that an epoxy group in destruxin E increases potency, while a COOH group may decrease potency, for example, destruxin D (Dumas et al., 1994). Agarwal and colleagues (1994) isolated and characterized destruxin B from the leaves of infected *B. napus* and established that the purified compound caused chlorosis of *B. napus* leaves. Bains and Tewari (1987) reported that this peptide induced necrosis and chlorosis in *Brassica* species, and suggested that the level of sensitivity of these plants to this compound was related to their degree of susceptibility to *A. brassicae*. Based on these observations, destruxin B is considered to be a virulence factor, contributing to the aggressiveness of *A. brassicae*.

Field trial results with Smolder[®], a bioherbicide (*Alternaria destruens*) for dodder (*Cuscuta* spp.) control, showed that 2.2×10^{10} viable conidia per hectare were required to reduce dodder in cranberry and carrot by at least 90 percent (Bewick et al., 2000). But the active phytotoxic mechanism for this bioherbicide is presently unknown. Risk assessment is needed to ascertain if this organism produces potent mycotoxins and if these mycotoxins are responsible for phytotoxicity.

COLLETOTRICHUM SPECIES

Colletotrichins. Colletotrichin, a norditerpene-pyrone, is a non-host-specific phytotoxin produced by species of *Colletotrichum* (Gohbara et al., 1977; Gohbara et al., 1978). Originally called acetylcolletotrichin (Grove et al., 1966), it is related to other analogs, colletotrichin B and colletotrichin C, which are precursors of colletotrichin (Kimura et al., 1978). Colletotrichin caused rapid membrane damage (cellular electrolyte leakage) in several crop plant and weeds, and the first ultrastructural symptom of phytotoxicity was loss of structural integrity of the plasma membrane (Duke et al., 1992). Colletotrichin reduces or prevents phytotoxicity of the synthetic herbicide acifluorfen (Gohbara et al., 1978). Acifluorfen requires a plasma membrane-associated redox enzyme for its activity (Jacobs et al., 1991), suggesting that colletotrichin may interfere with plasma membrane function. Colletotrichin is also produced by *C. gloeosporioides* Penz., the

causal agent of anthracnose symptomatology in mango leaves, and this compound inhibited seed germination in two non-hosts, lettuce and tobacco (Jayasankar et al., 1999). We are unaware of studies to detect or reports of production of this phytotoxin in other *C. gloeosporioides* pathovars or *Colletotrichum* species used as bioherbicides. Studies on colletotrichin are sparse, but in animals it inhibits mitochondrial respiratory electron transport (Foucher et al., 1974).

FUSARIUM SPECIES

Enniatins. Enniatins are cyclohexadepsipeptides produced by various strains of *Fusarium*. Their structures contain three residues of D-2-hydroxy-isovaleric acid (D-HIV) and an *N*-methyl-L-branched chain amino acid, in an alternating arrangement. Enniatin synthetase, a 350 kDa multifunctional enzyme, is the key in this biosynthetic pathway. Enniatins exhibit antibiotic properties against some bacteria and fungi due to their ionophoric properties. These compounds also inhibit mammalian cholesterol acyl transferase and are released as phytotoxins during plant infection by *Fusarium* spp. (Herrmann et al., 1996).

Fumonisinins. Fumonisin B₁ (FB₁) is a mycotoxin produced by saprophytic *Fusarium* species (Abbas et al., 1991; Abbas, Vesonder et al., 1992). It is also a phytotoxin and is also produced by an *Alternaria alternata* strain responsible for stem canker of certain tomato varieties (Chen et al., 1992). FB₁, first isolated from *F. moniliforme* MRC 826 (Bezuidenhout et al., 1988), is a hydroxylated, long-chain alkylamine containing two tricarboxylic acid moieties. It exhibits phytotoxicity to many weed and crop species (Abbas, Paul et al., 1992; Abbas, Vesonder et al., 1992; Tanaka et al., 1993; Van Asch et al., 1992). Ultrastructural and physiological studies of jimsonweed leaves treated with FB₁ indicated disruption of the light-dependent plasma membrane and tonoplast (Abbas, Paul et al., 1992; Tanaka et al., 1993). Fumonisinins and AAL-toxin have similar activity on plants, but AAL-toxin is generally more potent (Tanaka et al., 1993). Aminoalcohols (hydrolysis products of fumonisinins), exhibit low phytotoxicity. FB₁ is also a potent mammalian toxin (Abbas, Gelderbloom et al., 1993; Shier et al., 1991) and sphingolipid synthesis (inhibition of ceramide synthase) is the apparent site of action (Wang et al., 1991). Sphingolipids, at

relatively high concentrations, can cause phytotoxicity symptoms similar to those of fumonisins and AAL-toxin (Tanaka et al., 1993; Vesonder, Labeda et al., 1992; Vesonder, Peterson et al., 1992).

Fusaric Acid. Fusaric acid is produced by phytopathogenic *Fusarium oxysporum* strains and by nonpathogenic *Fusarium* species that grow saprophytically on maize kernels (Abbas et al., 1989). Fusaric acid is herbicidal against several weeds, including jimsonweed (Abbas et al., 1991; Abbas, Boyette et al., 1995) and duckweed (Vesonder, Labeda et al., 1992).

Moniliformin. Moniliformin occurs in isolates of saprophytic *Fusarium* species, and in pathogenic *Fusarium oxysporum* isolates (Abbas et al., 1989). Moniliformin causes growth inhibition, necrosis, and chlorosis in many weeds (Abbas et al., 1991; Abbas, Boyette et al., 1995; Vesonder, Labeda et al., 1992), but it lacks selectivity and also is highly toxic to mammals. It served as a template in the design and synthesis of compounds for herbicide discovery (Fischer and Bellus, 1983), but the synthetic herbicidal compounds obtained possessed high mammalian toxicity and were abandoned.

Trichothecenes. Trichothecenes are products of some common fungi, mostly *Fusarium*, but also species in the genera: *Acremonium* (*Cephalosporium*), *Cylindrocarpon*, *Dendrodochium*, *Myrothecium*, *Trichoderma*, and *Trichothecium*. Trichothecenes are tetracyclic sesquiterpenes containing a six-membered oxane ring; a stable epoxide group at positions 12 and 13; and a 9,10 olefinic bond. They have been classified into four groups. Trichothecenes cause hemorrhages, immunotoxic effects, and are potent protein-synthesis inhibitors in mammalian cells.

Macrocyclic trichothecenes also possess a wide range of phytotoxic specificity. Verrucarins A and J, and trichoverrin B, exhibit phytotoxicity in wheat coleoptile bioassays at low concentrations, and roridin A was phytotoxic to tobacco, corn, and bean seedlings (Cutler and Jarvis, 1985). Simple trichothecenes, such as neosolinol monoacetate and diacetoxyscripenol, were phytotoxic to pea seedlings, but wheat was tolerant (Brain et al., 1961). A *Myrothecium verrucaria* isolate that produces verrucarins also has efficacious bioherbicidal activity (Anderson and Hallett,

2004; Boyette et al., 2002; Hoagland et al., 2004; Walker and Tilley, 1997). More data and future research protocols on the development of this fungus as a bioherbicide have recently been published (Hoagland et al., 2007). Another *M. verrucaria* isolate from leafy spurge (*Euphorbia esula* L.) has a different weed host specificity, but also produces trichothecenes (Yang and Jong, 1995a, 1995b).

Zearalenones. Zearalenone and zearalenol are estrogenic resorcylic acid lactones produced by *Fusarium* spp. (Diekman and Green, 1992). Despite their structural dissimilarity to the steroidal estrogens, zearalenone and several analogs possess estrogenic activity. Zearalenone undergoes a molecular folding that favorably orientates hydroxyl groups to facilitate binding to estrogen receptors. Receptor binding affinities for zearalenone have been determined in sheep and calf uteruses (Diekman and Green, 1992). Zearalenone was genotoxic and carcinogenic in mice (but not rats), and affected reproduction and hormonal production in mice and rats. Alpha-zearalanol, closely related to alpha-zearalenol, a major metabolite of zearalenone, caused hormonal alterations in monkeys (Eriksen and Alexander, 1998).

OTHER FUNGAL PHYTOTOXINS

Cercosporin. Cercosporin, produced by several species of *Cercospora*, and isocercosporin, produced by *Scolecotrichum graminis* (agent of leaf streak in orchard grass [*Dactylis glomerata* L]) (Tabuchi et al., 1991), are photodynamic compounds. In the presence of sunlight and molecular oxygen they produce singlet oxygen (Hartman et al., 1988). Other photodynamic compounds, such as hypericin (a plant product) (Knox and Dodge, 1985), have been suggested as herbicides; however such compounds may be of high risk since they are toxic to life forms existing in sunlight and oxygen. On the other hand, various synthetic herbicides (paraquat, acifluorfen, pyridazinones, etc.) also generate toxic oxygen radicals.

Aflatoxin. Aflatoxins are mycotoxins produced by certain strains of *Aspergillus flavus*, *A. parasiticus*, and *A. nominius*. Although these fungi are ubiquitous, they do not always produce aflatoxin. Toxin production is dependent on environmental conditions (moisture, temperature, nutrient availability) and

related to fungal growth and strain genetics (Kacholz and Demain 1983). Aflatoxin is a contaminant in various food and feed products, and a risk factor for human liver cancer (Wogan, 1992). Aflatoxin B₁ is one of the most potent mutagens and carcinogens yet discovered, while other analogs are less toxic (Budavari, 1996). Plant tests of aflatoxins indicate they are also phytotoxic (Lilley, 1965; McLean, 1994; Schoental and White, 1965). Aflatoxins are absorbed by plants and translocated to and distributed within specific cellular compartments (McLean, 1993; McLean et al., 1994). Studies on aflatoxin metabolism in plants indicate either a lack of metabolism (Mertz et al., 1980; Reiss, 1984) or the detection of metabolites (Howes et al., 1991; McLean, 1993).

Risks Associated with Bioherbicides

Generally, risk can be defined in several ways, depending on the subject parameter at issue. But what is “risk” as related to bioherbicides? In most instances, risks associated with bioherbicides would include such concerns as worker exposure and safety, plant host-range, effects to nontarget organisms (competition/displacement of beneficial microbes in the community), carryover effects, and production of chemicals that are persistent or toxic to mammalian systems. These are some of the factors generally addressed in this overview. Some of these factors have been evaluated in certain instances with regard to bioherbicides, but often there are no apparent tests or published data available on these biocontrol agents. Several examples in which bioherbicidal risk has been published will be presented below.

Puccinia melampodii, a rust fungus isolated in Mexico, was approved for release in Australia in an integrated strategy to manage the highly allergenic weed, *Parthenium hysterophorus*, even though it could also sporulate on several marigold and sunflower cultivars (Evans, 2000). The Australian Quarantine and Plant Inspection Service concluded that the actual and potential hazards involved in not attempting to control this weed were significantly greater than the perceived risks to nontarget plants. During registration of *Colletotrichum gloesporioides* as Collego[®], extensive testing evaluated possible risks to humans and animals. Various animals were challenged with this phytopathogen via oral, dermal, nasal, ocular,

and interperitoneal injection (TeBeest and Templeton, 1985). Autopsies of all animals indicated no chronic symptoms and no infections. Environmental safety tests of Collego[®], with regard to nontarget plants and organism survival, were also conducted (Daniel et al., 1973; TeBeest et al., 1978). *P. palmivora*, DeVine[®], was also evaluated in animal toxicological tests including oral, interperitoneal injection, inhalation, eye, and skin (TeBeest and Templeton, 1985). However, toxic chemical profiling for possible mammalian toxins, or microbial displacement evaluations, were performed in the examples above.

There were two early commercial successes of microbial biocontrol agents: *Colletotrichum gloeosporioides* f. sp. *aeschynomene* (Collego[®]) for management of northern jointvetch (*Aeschynomene virginica* L.) in rice and soybeans, and *Phytophthora palmivora* (DeVine[®]) for management of stranglervine (*Morrenia oderata* H. & A.) in citrus orchards. DeVine[®] produces a lethal root rot and can persist saprophytically for extended periods, providing residual control over more than one year. Indeed, this is considered a marketing constraint since a single application may provide weed control over several growing seasons (Smith, 1982). *C. gloeosporioides* f. sp. *aeschynomene* produces lethal stem and foliage blight, persisting in dead host shoot and root tissues. It must be reapplied each growing season, which is beneficial to the marketer, but not to the consumer. The saprophytic nature of these agents also allows them to be produced in large quantities on simple media. Growth of these bioherbicidal microorganisms can occur over a relatively wide range of temperature and moisture levels, thus improving their field use. They are also genetically stable, and their target weeds are highly susceptible to them.

Commercial synthetic herbicides act against multiple weed species, but generally bioherbicides are host-specific, and act on only one weed or a few closely related species. Unless the target weed is a major problem, e.g., barnyardgrass [*Echinochloa crus-galli* L. Beauv] in rice, the biocontrol agent is likely to be too expensive to use for just one weed. The use of broad-spectrum bioherbicides such as *Myrothecium verrucaria* has recently been considered for invasive weeds such as kudzu (*Pueraria lobata*), which infests millions of hectares in the southeastern United States (Boyette et al., 2002). Although several plant species (Walker and Tilley,

1997) can be hosts of this pathogen, kudzu's dense growth habit and the fact that it usually doesn't flourish in extensive agronomic areas limits biological or economical concerns.

The host range of some bioherbicides can be altered through formulation or genetic modifications. The host range of *Alternaria crassa* (a pathogen specific for jimsonweed [*Datura stramonium*]) was expanded to include hemp sesbania (*Sesbania exaltata*), Eastern black nightshade (*Solanum ptycanthum*), showy croton (*Crotalaria spectabilis*), and cocklebur (*Xanthium* spp.) by addition of water-soluble extracts of weeds or fruit pectins to spore preparations (Boyette and Abbas, 1994). Although the host range was also altered to include some solanaceous crops, the pathogen could still be used with these crops if the timing of the applications was carefully considered. Formulation with invert emulsions expanded the host range of *Alternaria cassiae* (Amsellam et al., 1990) and *Colletotrichum truncatum* and *C. gloeosporioides* f. sp. *aeschynomone* (Boyette et al., 1991; Boyette et al., 1992).

All strains within a genus do not produce similar metabolites. It has been shown that inter- and intraspecific variation occurs regarding the quantity and types of toxins produced (Amiri-Besheli et al., 2000; Bandani et al., 2000). Furthermore, the types and quantities of toxins produced in liquid culture may have no relationship to metabolites produced in the plant host, or that are released into the environment (Abbas et al., 2001). Some strains of a given bioherbicidal microorganism may produce low amounts of mammalian toxicants unrelated to pathogenesis and thus these isolates would be attractive candidates to pursue as commercial products for weed control.

Knowledge of pathogen efficacy and data on the fate of inoculum and major toxic metabolites secreted is important. This information will provide insight as to the expected degree of weed control, safety concerns, and limitations of the product. It will also help promote worker safety and consumer confidence regarding bioherbicidal safety. To achieve these goals several key actions should be pursued (adapted from Strasser, 2000) as outlined below:

1. Develop protocols to detect trace amounts of toxic bioherbicidal metabolites.

2. Evaluate timing, application method (directed, broadcast, etc.) and product formulation, and so forth to minimize/eliminate organism or metabolite carryover into the human food chain.
3. Select microbial strains that are intrinsically poor mammalian toxin producers.
4. Identify parameters that regulate key metabolite production.
5. Develop diagnostic assays to provide data for bioherbicide registration and environmental fate.
6. Develop high-throughput assays to evaluate metabolite biochemical and toxicological modes of action. This will be useful in strain selection, predicting biocontrol range, and determining roles in antagonism/pathogenesis.

Fungi and bacteria are ubiquitous and encompass an extremely vast diversity of taxa with innumerable biological activities and interactions. There has been considerable interest in the development of some of these microorganisms as bioherbicidal agents (Charudattan, 2001), as well as for biocontrol agents against insects, nematodes, and plant pathogens (Charudattan, 2001). With respect to bioherbicides, many of these microorganisms are also pathogens to many crops, ornamentals, trees, and other nontarget plants; and they may cause allergies, toxicity, and pathogenicity that can affect the health of mammals. Considerable progress has been made in recent years in the development of environmentally benign fungal biological control agents for the control of weeds, insect pests, and diseases (Butt et al., 1999). Comparatively little bioherbicidal development has been done using bacteria versus fungi.

One of the major hurdles in registration and commercialization of microbial biocontrol agents has been in risk assessment, particularly that of secreted metabolites. Fungi secrete a wide range of metabolites, some of which are important medicines or research tools (Vey et al., 2001). Some of these metabolites are highly toxic (fumonisins, ochratoxins, patulin, zearalenone) or carcinogenic (moniliformin, aflatoxin). A large amount of data has accumulated on mycotoxin contamination of foodstuffs and the risk these metabolites (mostly from saprophytic fungi) pose to human and animal health (Abramson, 1998). Furthermore, various protocols have been developed to detect mycotoxins in the food chain (Wilson et al., 1998). In contrast, less is known

about metabolites from fungal biocontrol agents, particularly those from commercialized mycoherbicides, mycoinsecticides, and mycoparasitocides (Strasser et al., 2000; Vey et al., 2001).

There is debate in defining registration criteria for fungal biological control agents (BCAs) and global harmonization of registration procedures. Several key issues remain unresolved that may impede exploitation of microbes as BCAs (Neale and Newton, 1998; Strasser, 2000). Besides the issue of toxic metabolites, there is the concern about the use of exotic strains. Most fungal BCAs are found worldwide, and exotic strains can be efficacious against indigenous pests (Butt et al., 1992; Butt et al., 1994). There is no obvious link between geographic origin, virulence, host specificity, and toxin profile (Amiri-Besheli et al., 2000; Bandani et al., 2000). As indicated earlier, metabolite profiles reveal the potential of individual strains, but in the field situation it is highly unlikely that specialist insect pathogens, unlike saprophytes, would secrete large quantities of toxins. Most European countries have their own evaluation priorities for registration for new BCAs (Organisation for Economic Co-operation and Development [OECD], 1998), but it could be argued that it is more realistic for countries to place emphasis on environmental data collected from large field trials. These countries want data on the fate of the BCA in the environment, and its impact on target and nontarget organisms. On the other extreme are countries that place more emphasis on risk assessment. They require detailed information on the pathological and toxicological risks of BCAs to man and other nontarget organisms found in studies that are often conducted under unnatural conditions. Further discussions of risk factors associated with fungal BCAs have been addressed (Butt et al., 2001).

Even though fungi and bacteria may, as a whole, possess many hazards, many species are routinely safely mass-produced and used for inundative augmentative control of arthropods, nematodes, and weeds without apparent detrimental environmental impact (Vey et al., 2001). It should be cautioned however that hazards should be assessed at all developmental stages of a bioherbicide development. Human exposure should be minimized to avoid possible allergenicity or worker toxicity. Protocols to monitor workers combined with procedures to minimize direct contact of workers with the biocontrol agent should be in place. The

final formulated product should maximize pathogen-targeting characteristics, while minimizing drift or exposure to applicators and other nontarget organisms. Potential dangers to nontarget organisms in the environment should also be evaluated.

There is significant interest in developing bioherbicides for use in crops, gardens, rights-of-way, parks, and the like. However, currently, risk assessment of such microbial agents is limited. A more thorough approach is needed to tackle this problem. This review shows that existing commercialized fungal BCAs, including bioherbicides, do not pose risks to health or the environment because they possess host specificity and do not secrete harmful amounts of toxic and/or recalcitrant metabolites. However, we emphasize the need for the development of simple, sensitive methods and tools to identify and quantify possible toxic metabolites. Protocols for monitoring stability, competency, and impact of bioherbicidal microorganisms released into the environment should also improve our understanding and assessment of risks to the overall microbial community.

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