



Biological Control of Weeds by Fungi: Challenges and Opportunities

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Abstract

Weed plants are one of the main constraints to agriculture and cause considerable crop yield loss besides reducing product quality and leading to health and environmental threats. In comparison to various weed management strategies, biological control—especially mycoherbicides—offer an innovative approach to address this problem. Today, the bio-control of weeds by mycoherbicide (either fungal spore suspension or their metabolites) has received significant academic attention and over the past few decades some of the high profile candidates became commercially available. Employing mycoherbicide proposes benefits including being environmentally friendly, cost effective, and identifying new herbicidal mechanisms. This review focuses on challenges that mycoherbicides encounter before their adoption. Besides, important factors in both selecting and improving a fungal strain as a mycoherbicide are reviewed. Additionally, using integrated weed management as complementary methods to elevate the efficacy of mycoherbicides have been considered.

Keywords: Weed Management; Agriculture; Biological Control; Mycoherbicides

Introduction

Weeds are regarded as unwanted and undesirable plants, associated with declines in crop yields and quality, causing health and environmental hazards and account for more than 30% of total losses caused by all the pests [1]. Weeds can reduce crop yields by an average of 12%, which translates to \$32 billion in losses per year [2].

Common methods of weed control that are, mechanical and chemical approaches, associate with some drawbacks including being: costly, energy intensive, troublesome, having undesirable effects to the environment, development of resistance and the potential for injury to non-target organisms. Hence, there is a necessity to search for and develop new, economically and environmentally sustainable weed control technology. Using plant pathogens as biological control agents is one of the well-known alternatives to manage weed plants in disturbed environments [3]. Generally, two basic methods are applied for biological control of weeds: the

classical and the bio-herbicide approaches. In classical strategy a natural predator or pathogen of a weed species is simply released into weed populations and the expectation is that it will be capable to persist, increase and disperse naturally throughout the entire weed population and provide ongoing reduction of the weed species population throughout an entire ecosystem [4]. On the other hand, the bio-herbicide approach (also referred to as the inundative strategy) utilizes indigenous plant pathogens such as fungal or bacterial suspensions that are isolated from weeds and are cultured to produce large numbers of infective propagules. These are applied at rates that will destroy the weed species within a managed area. Annual applications of bio-herbicides are vital since the plant pathogen does not generally survive in adequate numbers between growing seasons [2].

Typically, in different studies, a wide range of organisms including nematodes, insects, bacteria, and fungi are used as bio-control agents. Biological control of weeds with phytopathogenic fungi of

fers prospects for overcoming several of the aforementioned inadequacies [5]. Scientific activity in mycoherbicide studies has increased significantly and application of registered or unregistered mycoherbicides has also expanded worldwide [6].

This review will focus on the use of mycoherbicide agents to control weeds and it will discuss incentives to develop this technology, factors that affect their efficacy in the natural environment, effects of mycoherbicides on weed plant physiology, and methods for improving fungi virulence toward weed plants.

Successful mycoherbicides

From 1960s until now, hundreds of different fungal strains throughout the world were assessed according to their competency to prevent invasive weed plants in both greenhouse and field conditions. The results of these studies have introduced several mycoherbicides for controlling some of the noxious weed species. Table 1 includes some of fungi with the high potential of phyto-pathogenicity. Besides, there are quite a few mycoherbicide candidates that have shown promise in greenhouse and/or field trials (Table

Bioherbicide agent	Target weed	Intended system	Stage of development	Country	Reference
<i>Colletotrichum gloeosporioides f.sp. aeschynomene</i>	<i>Aeschynomene virginica</i> (Northern jointvetch)	Croplands	Registered as Collego, no longer available	USA	[12]
<i>Colletotrichum gloeosporioides f.sp. malvae</i>	<i>Malva pusilla</i> (Round leafmallow)	Croplands	Registered as BioMal	Canada	[13]
<i>Phoma chenopodica</i>	<i>Chenopodium album</i> (Lamb'squarters), <i>Cirsium arvense</i> (Creepingthistle), <i>Setaria viridis</i> (Greenfoxtail), <i>Mercurialis annua</i> (Annual mercury)	Croplands	Research phase	Italy	[14]
<i>Phoma macrostoma</i>	Dicot plants	Turf	94-44B strain registered with EPA and PMRA in 2011	Canada	[15]
<i>Sclerotinia minor</i>	<i>Taraxacum officinale</i> (Dandelion), <i>Trifolium repens</i> (White clover), and <i>Plantago minor</i> (Broad leaf plantain)	Turf	Registered as Sarritor, no longer available	Canada	[16]
<i>Chondrostereum purpureum</i> strain HQ1	Re-growth of deciduous trees and shrubs	Woodlands	Registered as Mycotech Paste with PMRA in 2002, and with EPA in 2005	North America	[8]
<i>Chondrostereum purpureum</i>	<i>Prunus serotina</i> (American bird cherry) and <i>Populus euramericana</i> (poplar)	Woodlands	Registered as BioChon, no longer available	USA, Canada, New Zealand	[17]
<i>Chondrostereum purpureum</i> strain PFC 2139	Re-growth of deciduous trees and shrubs	Woodlands	Registered as Chontrol Paste with EPA in 2004, and with PMRA in 2007	North America	[8]
<i>Puccinia canaliculata</i>	<i>Cyperus esculentus</i>	Croplands	Registered as Dr. BioSedge	USA	[18]
<i>Alternaria destruens</i>	<i>Cuscuta</i> spp. (Dodder species)	Croplands	Registered as Smolder G and Smolder WP with EPA in 2005, no longer commercially available	USA	[19]
<i>Alternaria sonchi</i>	<i>Sonchus arvensis</i> (Perennial sowthistle)	Croplands	Research phase	America, Europe	[20]
<i>Phytophthora palmivora</i>	<i>Morrenia odorata</i> (Strangler vine)	Citrus orchards	Registered as DeVine (No longer commercially available)	USA	[21]
<i>Fusarium solani</i>	<i>Orobanche aegyptiaca</i> (Egyptian broomrape)	Croplands	Research phase	India, Israel	[22]
<i>Nimbya alternantherae</i>	<i>Alternanthera philoxeroides</i> (Alligatorweed)	Aquatic, up-land sites	Research phase	Worldwide	[23]
<i>Myrothecium verrucaria</i>	<i>Brunnichia ovate</i> (Redvine), <i>Campis radicans</i> (Trumpet creeper), <i>Pueraria lobata</i> (Kudzu)	Croplands, wastelands, natural areas	Research phase	Southern U.S.	[24]

Table 1: A list of either successful or potential candidates of mycoherbicides.

1). Some specific genera of fungi, such as *Colletotrichum*, *Phoma*, *Sclerotinia*, *Alternaria*, *Fusarium* and *Puccinia* received the majority of attention as bioherbicide candidates [7].

The mycoherbicide product Myco-Tech™ (*Chondrostereum purpureum*) was registered in 2002. This pathogen is an important fungal species which causes severe disease in many tree species in North America and is liable for the birch dieback in North American forests to a great extent [8].

The mycoherbicide DeVine is a formulation of the fungus *Phytophthora palmivora* that was twice registered in 1981 and 2006. The fungus was isolated from *Morrenia odorata* (strangler vine) in Florida and was applied to control the same plant. Though the product was re-registered in 2006, due to the limited market, it is not commercially available now [9].

One of the most promising aspects of using mycoherbicides is that they are cost beneficial. According to Page and Lacey (2006), the aggregate results of benefit/cost ratio (B/C ratio) for many mycoherbicide indicate an overall B/C ratio of 23:1 [10]. In another project for controlling *Chondrilla juncea*, the evaluation of B/C ratio of utilized fungal pathogens to control this weed, it was found that the accrued benefits to the users have been significant such as a 100:1 to 200:1 [11].

Phytotoxins

Fungi are well known for their ability to produce various phytotoxic metabolites with herbicidal characteristics. They including, but not limited to, various classes of natural compounds such as amino acids, aromatic, ethanones, nonenolides, furopyrans, trichothecenes, spirophytotoxins, coumarins and isocoumarins [25]. Table 2 shows a list of mycoherbicide phytotoxins that strongly target a number of weed plants.

Pathogen	Weed target	Phytotoxin	Mode of action	Reference
<i>Cantharellus cibarius</i>	<i>Eichhornia crassipes</i>	5-Methyl-Trp	Trp synthase	[30]
<i>Alternaria tenuis</i>	<i>Galium aparine</i>	Tentoxin	CF1 ATPase	[31]
<i>Preussia fleischhakkii</i>	<i>Arabidopsis thaliana</i>	Cyperin	Protoporphyrinogen oxidase and Lipid synthesis	[32]
<i>Alternaria alternata</i>	<i>Lemna pausicostata</i>	AAL-toxins	Ceramide synthase	[33]
<i>Fusarium spp.</i>	<i>Lemna pausicostata</i>	Fumonisin	Membrane functions and lipid stability	[33]
<i>Nectria sp. DA060097</i>	<i>Amaranthus retroflexus</i>	Cinnacidin	Unknown	[34]
<i>Gibberella fujikuroi</i>	<i>Arabidopsis thaliana</i>	GA mimic	GA3	[35]

Table 2: A list of molecular target sites of fungal phytotoxins.

During last decades, weed researchers have dedicated considerable time and expenditures in chemically characterizing many phytotoxins, yet in comparison to the opportunities, trivial efforts have been made to evaluate their weed control capacity [26].

Studies on Chenopodolin, a phytotoxic metabolite from *Phoma chenopodicola*, have shown that it has the capability to cause extensive necrotic lesions on lamb's quarter (*Chenopodium album*), creeping thistle (*Cirsium arvense*), green foxtail (*Setaria viridis*) and annual mercury (*Mercurialis annua*) [14].

Tentoxin is another fungal phytotoxin which was extracted from several *Alternaria* species. Duke., et al. reported that when tentoxin was applied against johnsongrass (in corn farm) and both broad-leaf and narrowleaf weeds (in soybeans farm), the phytotoxic metabolite provide a considerable weed control activity by causing severe chlorosis [27]. Furthermore, two phytotoxins, ascaulitoxin and trans-4-aminoproline, from fungal species *Ascochyta caulina* were isolated and proposed as bioherbicide agents against *Chenopodium album*. As a companion agent, the toxin solutions along

with the fungal spore suspension showed promising results in controlling the troublesome weed plant [28].

Another phytotoxic metabolite, named ascosonchine, was isolated from culture filtrate of fungal pathogen *Ascochyta sonchi*. The toxin was proposed as a potent biocontrol agent against *Sonchus arvensis*, that is one of the most important perennial weeds of agrarian crops [29].

Improving the mycoherbicide agent

As we discussed earlier, for assessing the potential of a mycoherbicide, weed researchers must consider some important characteristics such as host specificity, ability to grow and sporulate on culture media, genetic stability and virulence. A large number of studies have shown that lack of these properties will lead to low success rates of mycoherbicide products in terms of commercialization [36]. As it has been declared before, microorganisms can naturally modify their phenotypic characteristics by manipulating their genetic pool [37]. Various genomic approaches have been evolved to track the molecular bases of these modifications. Stuke-

nbrock., *et al.* (2008) mentioned scenarios such as horizontal gene transfer and hybridization as the possible processes which could lead to the emergence of either new host range or virulence in microorganisms and these scenarios, eventually, could result in birth of new plant pathogens [38]. As a matter of fact, molecular biologists used the clues, such as naturally occurring horizontal gene transfer and developed many methods to perform these processes in the laboratory to evolve fungi with high aggressiveness and host specificity toward intended weed plants. There are many techniques which have been prosperously applied to introduce foreign DNA into fungal species including electroporation, utilizing calcium chloride and polyethylene glycol, restriction enzyme mediated integration, lithium acetate and transformation by *Agrobacterium* [39]. There are limited examples of fungal transformation to elevate the potency of mycoherbicide. Dickman., *et al.* (1989) showed that transferring of cutinase producing gene from *Fusarium solani* to a species of *Mycosphaerella* could transform this fungus to a phytopathogen that could cause severe lesions on papaya plant [40]. In fact, after this study, there have been several articles of transforming different fungi to create strong mycoherbicides [41].

Cohen., *et al.* (2002) stated that up-regulation of indole acetic acid production in *Fusarium oxysporum* by transforming with *iaaH* and *iaaM* genes could double the efficacy of the mycoherbicide [42]. In another study, Amsellem., *et al.* (2002) declared that by transforming *Colletotrichum coccooides* with necrosis and ethylene inducing gene (NEP1) from *F. oxysporum*, a 9-fold increase in pathogenicity and a reduction of dew period requirement against *Abutilon theophrasti* attained [43].

Effect of fungal bioherbicides on weed physiology

Though a few researches have been run to clarify the physiological aspects of weed-fungi interaction during mycoherbicide treatments, some studies have underlined important metabolic processes, such as ones related to photosynthesis, hormones, antioxidants and nutrient uptake [44].

Fungal species inhibit weed plant growth by different mechanisms. For example, pathogenic fungi *Phoma macrostoma* attacks, colonizes and passes into the root part of the weed plant and develop its mycelium in the vascular trachea to obstruct the food uptake. *Curvularia intermedia* by producing the phytotoxin α,β -dehydrocurvularin hinders mitosis in cells of root tip and inhibits seedling development [45]. Besides, pectinase producing fungi can penetrate the cell wall of the weed plant by tearing apart the polysaccharide layers, enlarging the pores and releasing many lethal molecules into infected weed plant cells [46]. Moreover, the extracellular lipases of fungal species use the stored lipids in the endosperm of plant seeds for growth [47].

Indole-3-acetic acid (IAA) is a natural hormone that many bacteria and fungi can produce. *Enterobacter* sp. I-3 is a gram-negative bacterium that produces and secretes high concentrations of IAA to weed plants. By doing so, the endogenous IAA of the plant will enhance which result in the synthesis of aminocyclopropane-1-carboxylate (ACC), a motivator of ethylene biosynthesis. In the end, ethylene causes a reduction in weed growth [48]. Although, fungi have the potential to be evaluate in this regard, studies related to assessing the role of fungal species IAA in weed control is in its infancy.

Photosynthesis is another important process of plants that could be considered as a potential target for mycoherbicides. Macrocin is a fungal metabolite which produced by genus *Phoma*. This phyto-toxin interfere with carotenoid production and results in increased phytone production. Consequently, the ratio of β -carotene to lutein will decline; this will leads to decreases in both chlorophyll synthesis and photosynthetic gas exchange [49].

Other phytotoxic compounds, including tenuazonic acid, isoten-uazonic acid, N2- β -D-glucopyranoside, trans-4-amino-D-proline, cercosporin, beticolin, Nep1, trichothecene, β -1,4-exoglucanase, glucosidase, xylanase, β -1,4-endoglucanase and organic acids are produced by pathogenic fungi to control germination and development of weeds [50]. Table 3 provides a list of pathogenic fungi along with their mechanisms of action on weed plants.

Integrated weed management

In many instances, mycoherbicides will not provide the satisfying results to obviate the problem of invasive weed plants. In these cases, scientists in the field of weed science have shown that integrated weed management, which includes, physical, cultural, chemical and biological methods, could be a promising option. In fact, numerous studies have shown the great potential of mycoherbicides in conjunction with other anti-weed agents. For example, in the field trail, Wandeler., *et al.* (2008) provided a systematic rust infection in creeping thistles (*Cirsium arvense*) by using weevils as an insect vector to apply *Puccinia punctiformis* against this weed [57]. In another research, instead of utilizing a single pathogen, a mixture of fungal species, *Phomopsis amaranthicola*, *Alternaria cassia*, *Colletotrichum dematium f.sp. crotalariae*, *Fusarium udum f.sp. crotalariae* were used to control three weed plant species (pigweed (*Amaranthus hybridus* L.), sicklepod (*Senna obtusifolia*) and showy crotalaria (*Crotalaria spectabilis* Roth.)) and in the end, the results of greenhouse study showed that after weeds inoculation with the mixture of fungi's spore suspension, all of the seedlings were killed in 7 days [58]. Furthermore, Caesar (2003) demonstrated a strong synergy between *Fusarium oxysporum* and *Rhizoctonia solani* either with larvae or adults of flea beetle for controlling *Euphorbia*

Pathogen	Bioherbicide stimulant	Mode of action on weed plants	Reference
<i>Alternaria alternata</i>	Spore and culture	Leaf blight disease and inhibit seed germination	[50]
<i>Colletotrichum coccodes</i>	Spore	Induce disease and POD activity	[51]
<i>Colletotrichum gloeosporioides</i>	Spore	High rate of mortality, dry weight reduction and reduce plant growth, anthracnose lesions in stems, polysaccharides changes in cell wall	[46]
<i>Curvularia eragrostidis</i> isolate QZ-2000	Spore and culture (α,β -dehydrocurvularin)	Inhibit seed germination, biomass, chlorophyll, photophosphorylation, Mg ²⁺ ATPase, mitosis of root tips, increase necrosis, mortality	[45]
<i>Epicoccum purpurascens</i>	Spore	Inhibit seed germination and disease induction	[52]
<i>Fusarium equiseti</i>	Spore	Inhibit seed germination and disease induction	[52]
<i>Fusarium oxysporum</i>	Spore (24-kDa protein (Nep1))	Disease induction, necrosis, ethylene production, inhibit seed germination and infect seed testa and endosperm	[53]
<i>Myrothecium roridum</i>	Spore and culture (β -1,4-exoglucanase, β -1,4-endoglucanase, glucosidase, xylanase and pectinase)	Inhibit seed germination, growth and disease	[54]
<i>Myrothecium verrucaria</i>	Spore	Inhibit weed growth, chlorophyll and induce disease	[55]
<i>Phoma macrostoma</i>	Spore	Inhibit weed growth and disturb root cells	[15]
<i>Phoma macrostoma</i>	Spore and culture (macrocidins)	Inhibit growth, chlorosis, photosynthesis, carotenoid Biosynthesis	[49]
<i>Pythium</i> spp.	Culture	Reduce weed emergence and increase weed seedling Mortality	[56]

Table 3: Mechanism of action of fungal bioherbicides on weed physiology.

esula/virgate. Moreover, mycoherbicides could exacerbate the efficacy of chemical herbicides [59]. Vurro., et al. (2001) proved that combination of herbicides with phytotoxins of *Ascochyta caulina* provide a better control of *Chenopodium album* [28]. Gressel (2010) points out that glyphosate is more frequently used along with plant pathogens in integrated weed control. He believes that the probable scenario behind this fact is that glyphosate is very capable to hamper various weed defense mechanisms [60]. Boyette., et al. (2008) showed that glyphosate and the fungus *Myrothecium verrucaria* had a synergistic relationship in controlling redvine (*Brunnichia ovata*) and trumpet creeper (*Campis radicans*) in a field study [24]. The mechanisms by which mycoherbicides synergize glyphosate are not quite clear yet.

Challenges for weed control by mycoherbicides

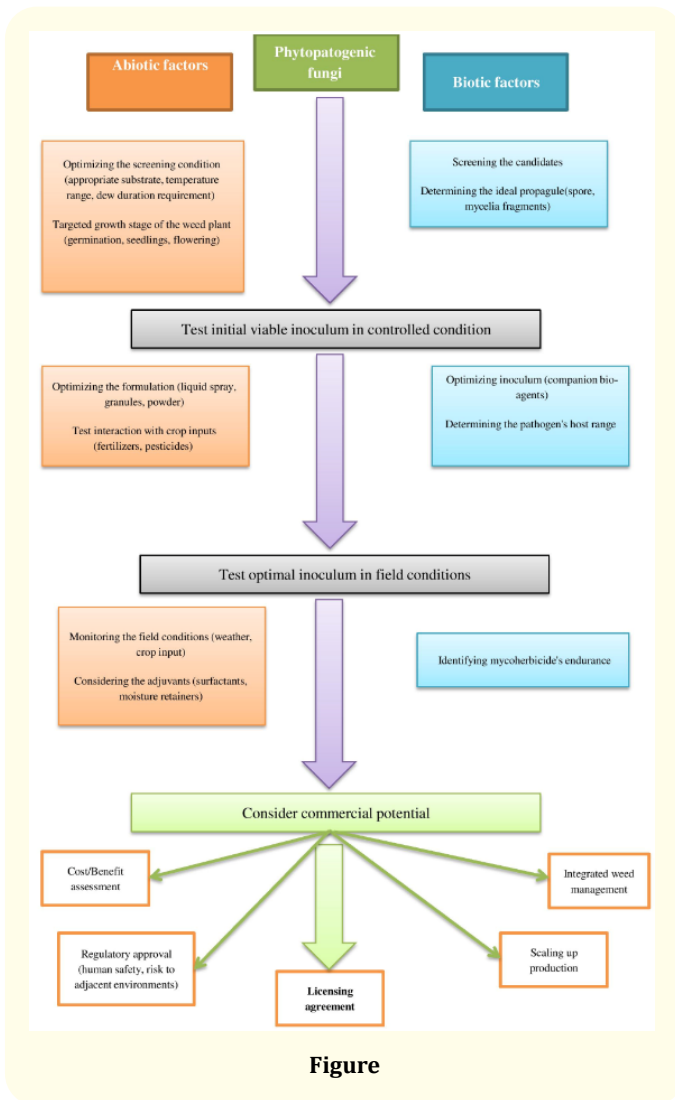
There are several challenges in developing a prosperous mycoherbicide (Figure 1). In fact, these challenges divide into economic, environmental or political categories.

One of the central challenges in using mycoherbicide agents to control weed plants is to finding suitable strategies of application

that allow the unvarying distribution of the agent at the desired site. The uniform and accurate application of microbial suspension close to the target weed would decrease the cost of treatment and the risks of non-target effects [61].

One of the most important problems related to the release of a mycoherbicide in the environment for weed bio-control is the lack of knowledge about the actual host range of the microorganism in the environment. Several studies have shown that some agents introduced for alien weed control have invaded non target plants [62] and this issue has resulted in raising concerns both among weed scientists and governments. For example, *Phytophthora palmivora*, the fungus formulated as Devine, was intended to target *Morrenia odorata*, but it also infects some non-target crops such as onion, cantaloupe, watermelon, okra, tomato, endive, cucumber, English pea, and carrot [63]. Thus, the host range and environmental impacts of mycoherbicides must be assessed thoroughly.

Another important factor in determining the potential of fungal strain as a mycoherbicide is that the phyto-pathogen must be easily culturable in artificial media; the pathogen must be able to propa-



Figure

gate using conventional approaches e.g. liquid fermentation and it ought to be genetically steadfast and specific to the intended weed plant [64].

The interaction of temperature and moisture also has a critical impact on the success or failure of myco-herbicide agent [65]. Due to the fact that relative humidity of cold air is higher than warm air, because of the lower rate of evaporation, thus the duration of leaf wetness will increase and consequently the efficacy of the mycoherbicide will invigorate [65]. According to the findings of a study that was carried out to assess the potential of mycoherbicide product Sarritor, it was shown that compared to warmer temperatures, the efficacy of the weed control agent was very high in temperatures below 20°C [66].

The fungal pathogen, *Phloeospora heraclei* showed a high potential to control giant hogweed (*Heracleum mantegazzianum*) *in vitro* based screening trials but the mycoherbicide's further evalu-

ation was ceased when it was discovered that it has a great tendency toward several related crop plant species [67].

The tendency toward utilization of mycoherbicides is dissimilar in different parts of the world. Investment on this technology in some countries, such as Canada and USA, is heavy [68], while in others such as New Zealand and European countries low number of projects has been funded on this topic [69].

Bio-herbicide approach has been known to be more economical in comparison with current technologies; However some specific reasons including: the long time frames for development and some disappointing examples of weed bio-control, have reduced the rate of their adoption [70].

Also, despite the promising examples of fungi that have shown high potential of weed control, scientific and legislative hesitations, along with undesirable public perception or cognition about pathogenic microorganisms (pathophobia), negatively influenced some countries, especially European countries in using these agents for weed control [69].

As a matter of fact, developing a prosperous mycoherbicide agent face quite a few challenges, and continued research and development are required to verify their capability as the alternative for weed management.

Conclusion

Biological control of weeds with mycoherbicides has been satisfactorily implemented for several important weed plants. Further researches are required to elevate our understanding of different aspects of weed-fungus interaction. By doing so, we will be able to apply new strategies to fight these noxious weeds. The most important factors related to having a perfect mycoherbicide product are: specificity, competitiveness, cost efficiency, and being environmentally sound. Producing new formulations and finding an efficient delivery system are vital to extend the shelf-life and efficiency of the mycoherbicide agent in different environmental conditions. Moreover, herbicidal activity of the mycoherbicide agents could be enhanced with research on strain selection criteria including genetically engineered fungal pathogen to create a mycoherbicide that is both more specific and more virulent. Weed control should not be considered a self-contained option but may be best if integrated with other approaches. In fact, Chemical herbicides and other biological agents such as insects could play a complementary role beside the mycoherbicide agent and, surely, they can invigorate the phyto-pathogenic potential of the final product.

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