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Scope and potential of herbicidal values of the fungal pathogens and its secondary metabolites for sustainable weed management

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Abstract: Weeds are the major menace to agriculture, which greatly impact crop growth and development, resulting in economic yield loss or crop failures. Therefore, it is indispensable to take up appropriate weed management practices to prevent the effects of weeds on crops. Chemical herbicides have immense potential for effective control of weeds, but, in the long run, the persistent nature of herbicides adversely affects the soil microbes and also that terrestrial and aquatic ecosystems. Bioherbicides are products derived from plant extracts, allelochemicals or microbes and their secondary metabolites with weed-suppressing abilities. Most microbial bioherbicides are based on fungi and its active ingredients, which successfully control weeds with different mode of actions. Moreover, the toxins or secondary metabolites the fungi produce also possess herbicidal properties. So, exploring the fungal pathogens and their toxins for managing weeds seems to be a feasible and eco-friendly way for the management of weeds. There is a wider scope for utilizing fungi and their secondary metabolites as mycoherbicides, which have the potential to replace hazardous chemical herbicides in the near future. This review article mainly emphasizes the scope of mycoherbicides and explores the fungal secondary metabolites for eco-friendly weed control.

Keywords: biological control; bioformulations; fungi; mycotoxins; weeds

Weeds are the main competitors to the crop for various resources like nutrients, moisture, light, space, etc. They are one among the biotic factors which cause severe yield reduction (45%), increase the cultivation cost and decrease the input efficiency when compared to other biotic factors like insects (30%), diseases (20%) and other pests (5%). An economic loss of around 11 billion USD has been estimated due to the infestation of weeds in 10 major crops of the Indian sub-continent (Gharde

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et al. 2018). Crop production is highly challenged by weeds, which have to be managed appropriately, or else they will result in a huge decline in the yield of the crops. The survey conducted by several weed scientists revealed that around 10–100% of yield loss was observed in major crops grown in India owing to severe weed infestation (Rao & Chauhan 2015). Due to the scarcity of labour in agricultural activities, chemical herbicides have become indispensable in modern cropping and farming systems. Unfortunately, improper and irregular application of herbicides paved the way for several environmental issues like herbicide resistance, groundwater contamination, soil health reduction, soil microflora exhaustion, loss of biodiversity, threat to human health, etc. So, to manage weeds effectively as well as to sustain the health of the ecosystem, the concept of biological control of weeds has to be adopted (Kubiak et al. 2022).

In the last four to five decades, many scientists have turned towards the biological approach of weed control through plant extracts, insects, pathogens, fish, etc. The trend of utilizing bioherbicides like allelochemicals secreted by plants and the use of fungal pathogens and their secondary metabolites or mycotoxins for the successful management of weeds has been advancing in recent days. Exudates of various plants and weeds have immense potential to limit the growth and development of various weeds. Likewise, numerous insects were also engaged in the management of some noxious and troublesome weeds. Various fungal pathogens naturally induce severe necrotic symptoms in diverse weed species. So, there is a possibility of inducing such infections in weeds through a mycoherbicidal approach. Several mycoherbicidal products have been registered and commercialized worldwide for weed management through an eco-friendly approach. In the near future, growers may rely upon mycoherbicide formulations to control the weeds as a sustainable approach. They possess enormous potential to manage problematic weeds efficiently without harming the ecosystem. Similarly, the culture filtrates and the toxins released by pathogens can also be utilized to manage the weeds irrespective of the environmental conditions. Several mycotoxins have been identified which effectively induce phytotoxicity on various weed species. So, in this review, prime emphasis is given to the utilization of fungal pathogens and their secondary metabolites, which have the potential to act as an alternative to chemical herbicides for the effective and eco-friendly management of weeds, thereby sustaining the ecosystem.

ENVIRONMENTAL HAZARDS DUE TO CHEMICAL HERBICIDES

Due to the constraints of agricultural labour, time, and cost, the chemical method of weed control has become inevitable for the instant management of weeds (Barman & Varshney 2008). The application of chemical herbicides significantly contributed to maximizing agricultural production to support vast populations all over the world. However, in due course of time, the indiscriminate application of herbicides has resulted in the persistence of toxic chemicals in soil and has posed serious hazards to the ecosystem.

Soil contamination. Soil comprises microorganisms like bacteria, fungi, actinomycetes and macroorganisms viz., earthworms, insects, spiders, nematodes, etc. This complex array of life forms is directly involved in various processes like decomposing residues, recycling and storing nutrients, and maintaining the soil structure, texture, stability and degradation of soil contaminants. The herbicide sprayed on the weed not only gets contact with it but also with the soil and its surrounding ecosystem. This might affect the rhizospheric microbes, soil-borne pathogens, pests, and disease antagonists. Generally, bacteria have a better ability to decompose the herbicides when compared to fungi and actinomycetes (Lone et al. 2014). The activity and count of soil microbes were encouraged in the soil deprived of herbicide application. Few studies recorded that the chemical nature, dosage, soil type, and sampling time played a major role in soil contamination by herbicides.

Application of herbicides viz., butachlor at the concentration 1.0 kg/ha, 2,4-D ethyl ester at the concentration 0.75 kg/ha and pyrazosulfuron ethyl at the concentration 25 g/ha reduced the count of total heterotrophic bacteria (Latha & Gopal 2010). Adhikary et al. (2014) reported that a transient decrease in microbial population was observed with the application of pendimethalin (3 300 mL/ha) and oxyfluorfen (850 mL/ha). Spraying acetochlor at different concentrations, viz., 1.25, 1.50, 2.50, 3.125 and 5.0 L/ha, lowered the count of soil bacteria, fungi and actinomycetes (Tyagi et al. 2018). Kumar et al. (2020) revealed that the application of

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the herbicide bispyribac sodium (35 and 75 g/ha) decreased the soil microbial population, microbial biomass carbon and the activities of soil enzymes. Ji et al. (2023) assessed the impact of atrazine on soil microbes and revealed that the application of atrazine lowered the population of soil microorganisms. Some findings have supported the fact that herbicide residues can serve as a carbon and energy source for microorganisms, while other reports claim that herbicide residues result in devastating effects on soil biology and chemistry. However, in the long term, it may disrupt the soil's biochemical balance, thus reducing soil fertility and productivity (Hussain et al. 2009; Marin-Morales et al. 2013). The active ingredients present in the herbicides affect the nitrite synthesis, nitrogen fixation and mycorrhizal process.

Aquatic toxicity. Because of the cumulative increase in the use of herbicides for controlling the weeds, the residual chemicals find their destination in the nearby streams, lakes and underground water sources through leaching and runoff mechanisms and jeopardize the health of the marine and aquatic ecosystem (Sondhia 2014). Furthermore, these chemical herbicides maximize the reproductive toxicity of various aquatic species (Yang et al. 2021).

Human health effects. Consumption of such chemicals results in severe health hazards for life forms, including humans, animals, etc. (Kubiak et al. 2022). Likewise, Balderrama-Carmona et al. (2020) disclosed that human beings exposed to chemical herbicides or consuming foods contaminated with residues of herbicides result in serious health hazards like infertility, neurotoxic effects, cytotoxicity, endocrine disruption, kidney problems, etc. Gupta (2022) stated that exposure to chemical herbicides affects the developmental processes and disrupts reproduction in humans and animals.

BIOLOGICAL APPROACHES OF WEED MANAGEMENT

Usually, weeds are managed by physical/mechanical/cultural/chemical/biological methods or their combination. Due to the shortage of agricultural labour, adverse effects of chemical herbicides, increasing rate of herbicide resistance, high cost involved in weed control methods, etc., have led to the preference for biological methods of weed control in the upcoming days. It has encouraged various agronomic scientists to formulate sustainable weed management approaches (Hershenhorn et al. 2016). Biological control suppresses weeds through biological agents or natural enemies (Figure 1). These agents may be plant pathogens (fungi, viruses, bacteria and nematodes), phytophilous arthropods (insects and mites), fish (grass carp), birds (geese) and other animals (sheep) (Westwood et al. 2018).

There are two strategies for biological weed control: classical (inoculative) and inundation (augmentation or bioherbicidal). The inoculative method deals with the introduction and exploitation of non-native or foreign agents to suppress an exotic aggressive weed in its new area of infestation, while the augmentation method deals with the exploitation of indigenous or native bio-agents to manage weeds by amplifying their population intensities beyond usual levels (Aneja et al. 2017; Bo et al. 2020).

MYCOHERBICIDES

Microbe-based bioherbicides, which particularly involve fungal pathogens and their secondary metabolites for the management of weeds, are termed mycoherbicides. The steps involved in the development of biological control of weeds with fungal pathogens are *(i)* extensive exploration for plant pathogens associated with the weeds, *(ii)* environmental studies and geographic features of the native or indigenous areas of the pathogen, which have a massive impact on disease infectivity (pathogen's ability to cause infection), intensity, virulence (severity of the infection caused by the pathogen) and the ability to extend its range from one plant to the other has to be considered and *(iii)* determining the safety of the pathogen by observing its taxonomic position and by carrying out host specificity (range and variety of host species on which the pathogen can incite infection) studies (Gupta & Mukerji 2000). The ideal characteristics of a potential mycoherbicidal pathogen have been depicted in Figure 2. Various processes involved in developing mycoherbicidal formulations with fungal spore suspension and fungal metabolites for managing weeds are illustrated in Figure 3.

POTENTIAL FUNGAL PATHOGENS FOR WEED CONTROL

Application of conidial suspension of *Curvularia lunata* (strain B6) at the concentration 1×10^4 to 1×10^6 per mL in rice fields at three leaf stage of the weeds effectively controlled *Echinochloa crus-*

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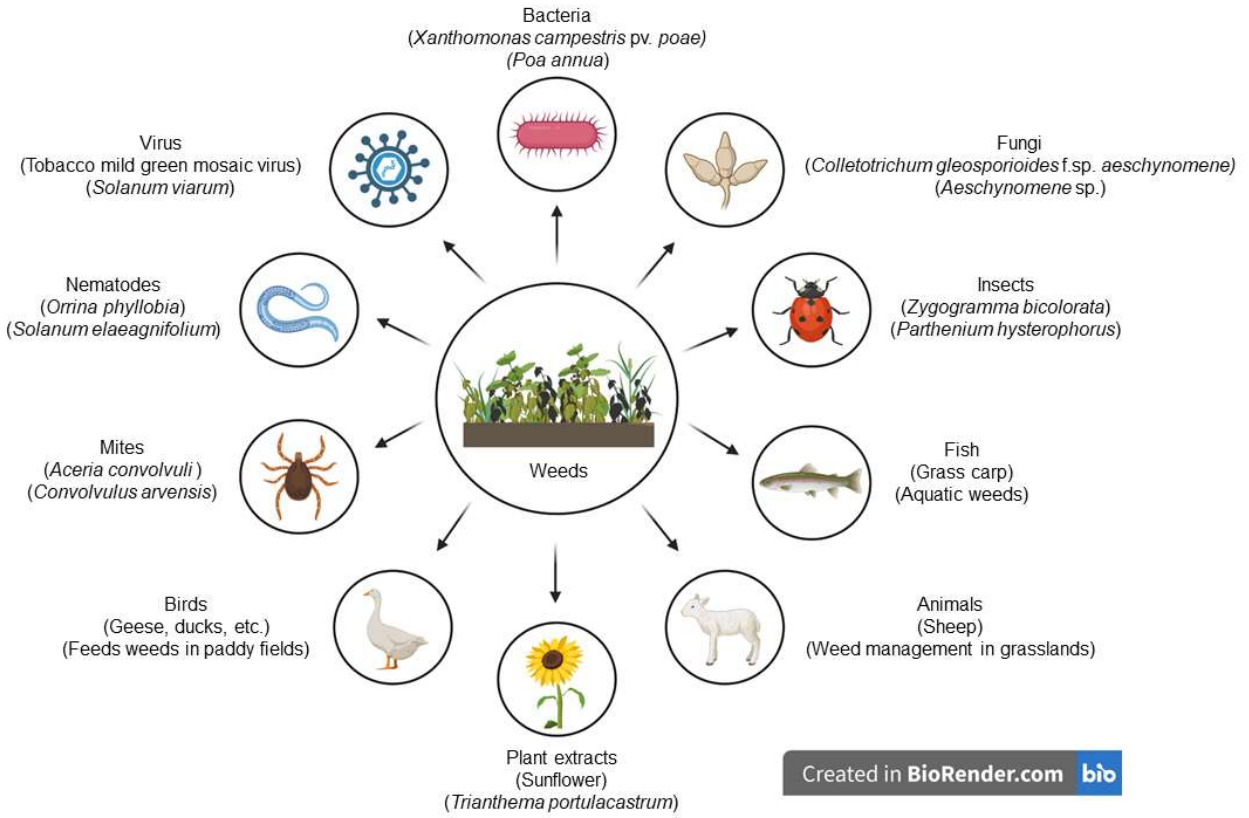

Figure 1. Various biological approaches employed for the management of weeds

Bioformulations prepared from plant extracts, fungi, bacteria and viruses can be successfully utilized for managing weeds. Similarly, insects, nematodes and mites can also be introduced into areas of severe weed infestation to control the specific weed species. Integrating fishes and ducks in lowland ecosystems (paddy fields) assists in managing the aquatic weeds. Likewise, animals like sheep can be exclusively used for managing the weeds in grasslands and roadsides

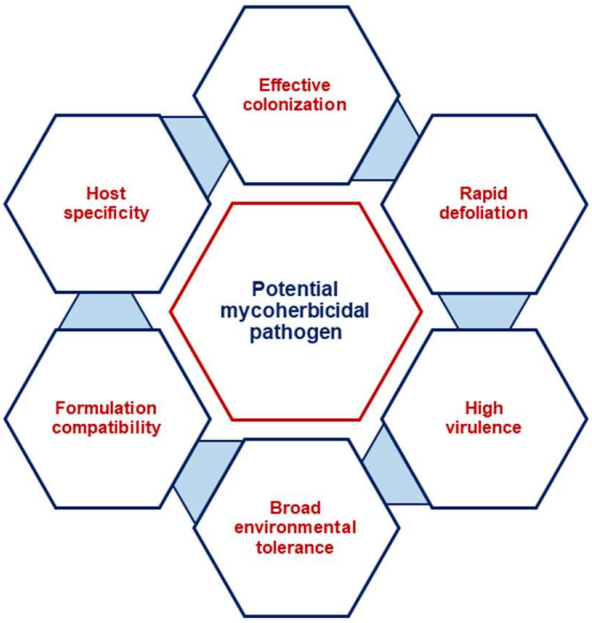

Figure 2. Ideal characteristics of a potential mycoherbicidal pathogen for effective weed management

galli (Jing et al. 2013). Spraying of spore suspension of the fungal pathogen, *Bipolaris eleusines* at the concentration 1×10^7 conidia per mL at three leaf stages resulted in severe mortality (73%) of *E. crus-galli* (Zhang et al. 2014). Inoculation of necrotrophic pathogen *Colletotrichum echinochloae* (isolate B-48) spore suspension at the concentration 1×10^7 spores per mL on *E. crus-galli* significantly reduced its fresh weight (Gu et al. 2023).

The fungal pathogens such as *Alternaria alternata*, *Fusarium oxysporum* and *Phoma herbarum* caused a severe infection on *Trianthema portulacastrum*. Among them, spraying of *P. herbarum* registered the maximum mortality of *T. portulacastrum* (Ray & Vijayachandran 2013). Inoculation of *Gibbago trianthemae* at the concentration 5×10^4 spores per mL effectively controlled *T. portulacastrum* (Mitchell 1988). Aneja et al. (2013) revealed that applying a conidial suspension of *G. trianthemae* at the concentration 2.2×10^5 conidia per mL to *T. portulacastrum* resulted in

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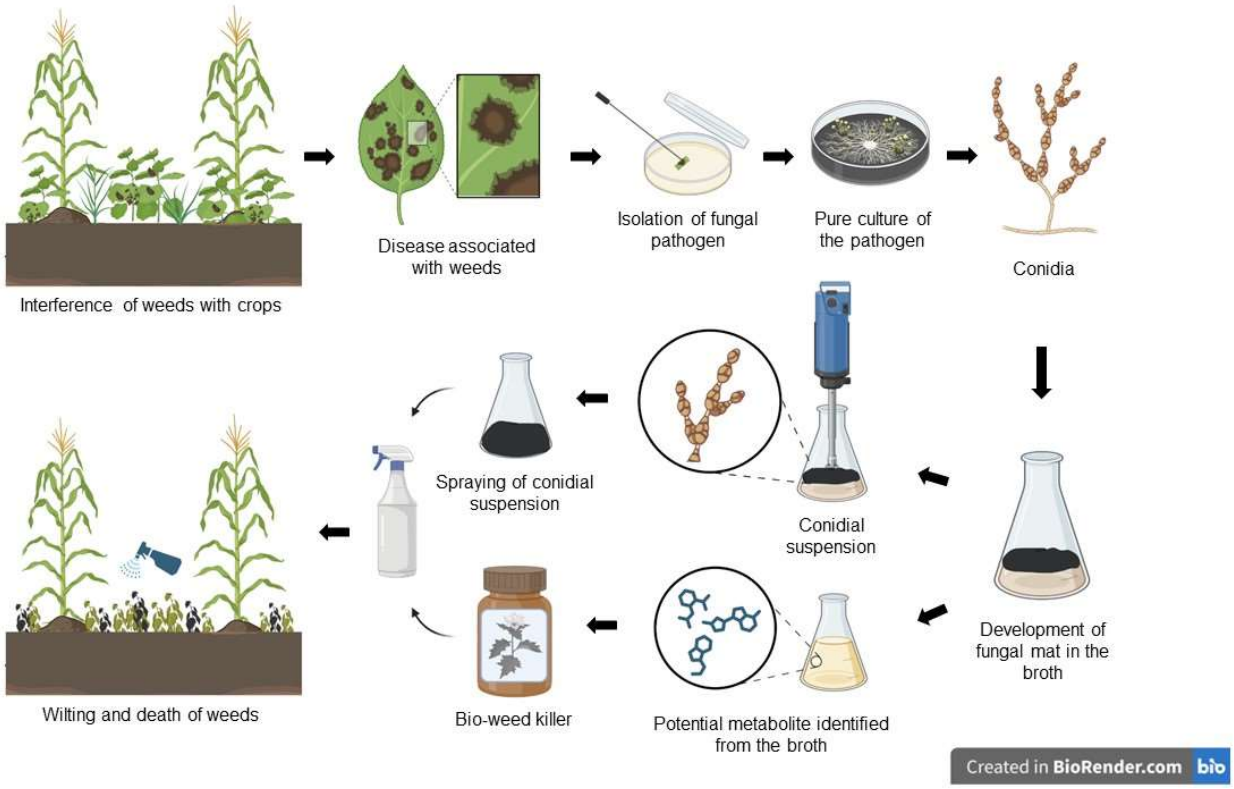

Figure 3. Steps involved in the development of mycoherbicidal formulation

severe defoliation. Gaddeyya and Kumar (2015) sprayed the conidial suspension of *G. trianthemae* at the concentration 5×10^4 spores per mL supplemented with surfactant (tween 20 at the concentration 0.02%) on *T. portulacastrum* and reported a percentage disease index of 95–98%. The post-emergence spraying of the liquid formulation of *G. trianthemae* at the concentration 10×10^6 spores per mL effectively controlled *T. portulacastrum* in maize crop (Sreeja 2022; Sreeja et al. 2022).

Isolates of *Sclerotium rolfsii* from *Parthenium hysterophorus* exhibited varied disease incidence percentages on *P. hysterophorus* and have the enormous potential to be developed as a mycoherbicide (Shukla & Pandey 2008). *In vitro* and *in vivo* studies carried out by Kumar et al. (2009) revealed that *Cladosporium* sp. (MCPL 461) can potentially control *Parthenium hysterophorus.* Spore suspension of *Cladosporium* sp. at the concentration 10^{10} to 10^{12} spores per mL sprayed on *P. hysterophorus* produced severe disease symptoms. Further, a 3% sucrose solution was added to the formulation to improve its mycoherbicidal activity, enhancing its efficacy. Application of spore suspension of the pathogen *Alternaria alternata* ITCC4896 at the concentration 1×10^6 spores per mL effectively controlled *P. hysterophorus* (Saxena & Kumar 2010). Kaur and Aggarwal (2015) controlled the troublesome weed *P. hysterophorus* biologically by developing mycoherbicidal formulations of *Alternaria macrospora*.

Application of conidial suspension of the pathogen *Nimbya alternantherae* at the concentration 1×10^5 and 1×10^6 conidia per mL effectively controlled *Alternanthera philoxeroides* under greenhouse and field conditions, respectively (Pomella et al. 2007). Lima et al. (2010) developed a conidial suspension of *Plectosporium alismatis,* and application of the spore suspension at the concentration of 2×10^6 and 2×10^7 conidia per mL produced the symptoms of leaf blight to the extent of 86% and 93%, respectively on *Sagittaria montevidensis*. Spore suspension of *Phaeoacremonium italicum* at the concentration 1×10^6 spores per mL produced 100% and 90% damage to *Eichhornia crassipes* around 144 h post inoculation in detached leaf assay and whole plant assay respectively (Singh et al. 2016).

A spray concentration of 10^7 *Alternaria alternata* spores per mL in rapeseed oil emulsion formulation applied to *Amaranthus retroflexus* plants resulted in

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complete mortality of the plants at four-leaf stage (Ghorbani et al. 2000). Spore inoculum of the fungal pathogen *A. alternata* (LC#508) sprayed at the concentration of 1.65×10^6 spores per mL caused mortality of *Lantana camara* in detached leaf assay, *in vitro* cut shoot assay and also *in vivo* bioassay (Saxena & Pandey 2002). The mycoherbicidal formulation prepared in canola oil emulsion (20%) with *A. alternata* spores at concentration 10^7 per mL effectively controlled *Chenopodium album* (Siddiqui et al. 2010).

Application of conidial suspension of *Myrothecium verrucaria* at concentration 2×10^7 spores per mL coupled with the surfactant Silwet at the concentration 0.2% to the weeds viz., common purslane, horse purslane, spotted spurge and prostate spurge at 2–3 leaf stage resulted in necrotic symptoms within 24 h of inoculation and after seven days of inoculation the pathogen killed almost 90–95% of both the purslane weed species and 85–95% of both the spurge weed species (Boyette et al. 2007). Lee et al. (2008) inoculated the spore suspension of the fungal pathogen *Myrothecium roridum* (F0252) at the concentration of 6.5×10^6 and 2.5×10^7 spores per mL to the seeds of white clover and ladino clover and the spore suspension greatly inhibited the germination of seeds and severely affected the seedling growth of the weeds under *in vitro* conditions. The mycoherbicidal activity of the pathogen was also evaluated under *in vivo* conditions, which displayed broad-spectrum herbicidal properties.

Fungal pathogen *Phomopsis cirsii* is highly pathogenic to the weed *Cirsium arvense,* causing the symptoms of dieback and stem canker, and the mycopathogen can be utilized as a potential mycoherbicidal agent against the host weed species (Leth et al. 2008). Toh et al. (2008) revealed that *Lasiodiplodia* sp. caused severe seedling mortality of *Parkinsonia aculeata* and can reduce the seed bank of *P. aculeata*. Cipriani et al. (2009) reported that *Fusarium oxysporum* is specific and extremely virulent to *Orobanche ramosa* and has the potential to be developed as a mycoherbicide. Application of spore suspension of the pathogen *Aureobasidium pullulans* at the concentration of 10^{16} spores per mL resulted in maximum infection of the weed *Chromolaena odorata* (Prashanthi & Kulkarni 2005). Conidial suspension of *Phoma multirostrata* at concentration 1×10^8 conidia per mL effectively induced disease symptoms on *Tridax procumbens* to the extent of around 60–98% under laboratory conditions and 65–87% under greenhouse conditions 15–20 days post inoculation of the spore suspension (Srisuksam et al. 2022).

Since the 1960s, various microbial bioherbicides have been registered and commercialized, of those majority of them were derived from the fungi such as Lubao, DeVine®, Collego™ (Lock Down®), Casst™, ABG-5003, Dr. Biosedge®, Velgo®, BioMal®, Stumpout™, BioChon™, Hakatak®, Woad Warrior®, MycoTech™, Chontrol™ (Eco-Clear™), Smoulder®, Sarritor™, Phoma®, Gibbatrianth and Di-Bak Parkinsonia®. The fungal pathogen(s) involved and the target weed(s) of the respective mycoherbicides are illustrated in Figure 4. Camperico™, Organo-sol® (Kona™/Bioprotec™), MBI-005 EP (Opportune™), D7® and Battalion Pro are bioherbicides based on bacteria. SolviNix™ is the only bioherbicide based on virus. The detailed description of the above-mentioned bioherbicides, like the time of registration and country, biocontrol agent involved, type of formulation, and their target weeds, were clearly specified by Cordeau et al. (2016), Aneja et al. (2017), Galea (2021) and Kremer (2023).

Several bioherbicidal products have been registered and commercialized to date, but only a few products are available in the market. This might be due to low consumer demand, cost involved in the mass production of formulations, inconsistent performance under field conditions, etc. So, to develop an effective and efficient mycoherbicide, the fungal pathogens possessing high virulence and the determinants of virulence must be recognized. The selected fungal agent should be well prepared to fit and adapt to the field conditions.

SUCCESSFUL EXAMPLES OF BIOLOGICAL CONTROL OF WEEDS

Management of *Striga hermonthica* in Kenya. *Striga hermonthica*, a partial root parasitic weed, depends on cereal crops for nourishment. Due to the severe infestation of this parasitic weed in sub-Saharan Africa, there was a massive reduction in the yield of crops, especially maize, which experienced severe impact due to the infestation of *S. hermonthica* and sometimes total crop failures have also been observed. The biological approach of utilizing the fungal pathogen, *Fusarium oxyspo-*

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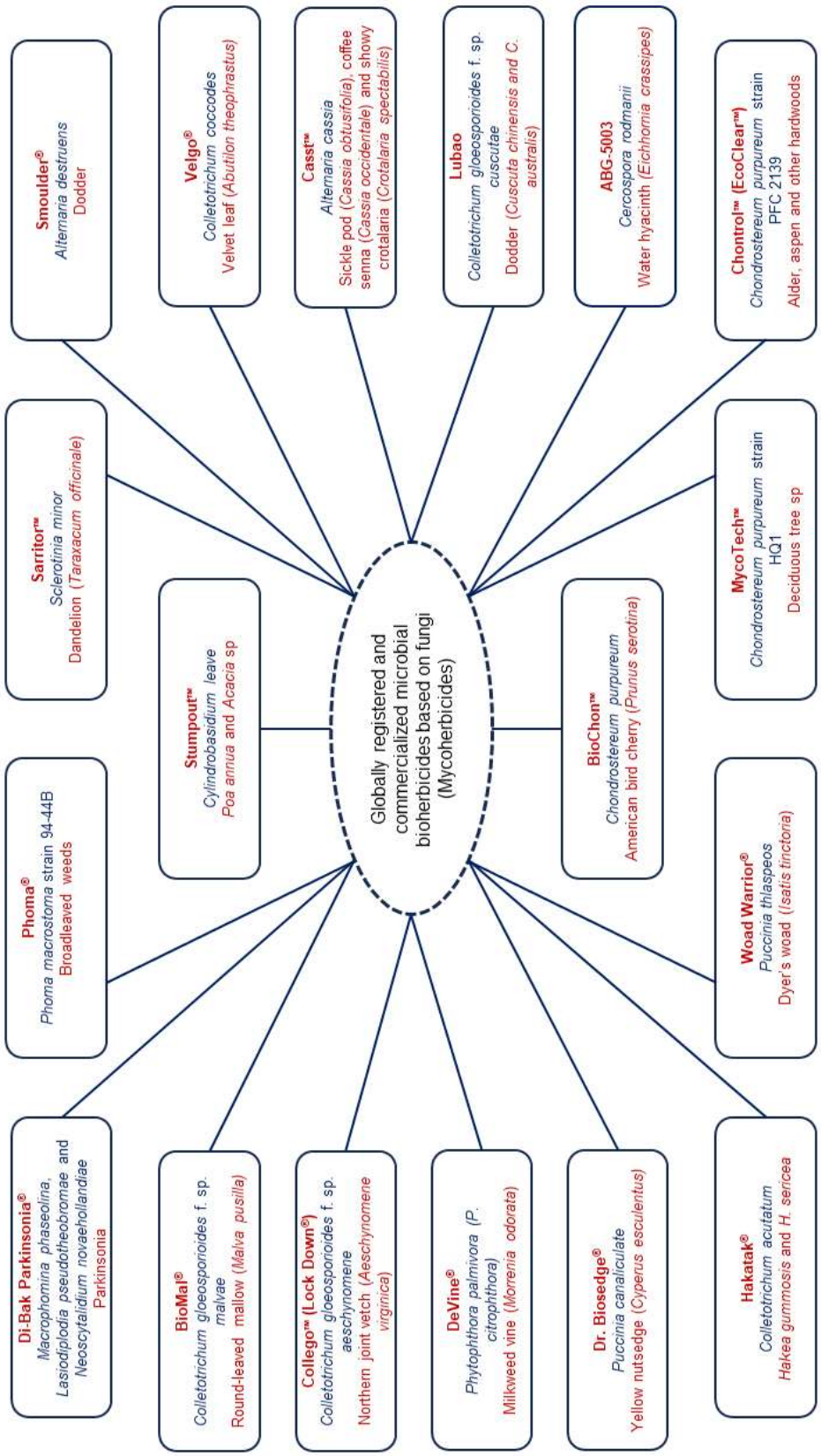

Figure 4. Registered and commercialized mycoherbicides, fungal pathogen(s) involved and its target weed(s)

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rum f. sp. *strigae*, was undertaken to manage the weed effectively. This pathogen selectively attacks *Striga* sp. without causing any effects on crops like maize, pearl millet, sorghum, rice, cowpea, groundnut, cotton, fonio and okra. Nevertheless, some plants of Solanaceae were susceptible to it.

The concept of amino acid toxicity was utilized here, and the amino acids that exclusively inhibit *S. hermonthica* but not maize were identified; they are tyrosine and leucine. The specific strains of the fungal pathogen *F. oxysporum* that overproduce the amino acids (tyrosine and leucine) were selected. In addition, the variants that overproduce methionine were also selected as the amino acid methionine gets converted into ethylene due to the activity of soil microbes, which assists in the germination of *Striga*. Three selected strains of fungal pathogen (Leu2a, Z6a and Z5a) that overproduce the amino acids viz., leucine, methionine and tyrosine were cultured individually on potato dextrose agar medium on which sterile wooden toothpicks were placed. The fungi grew and ramified on the toothpicks. Then, they were dried aseptically in a laminar flow cabinet, and after complete drying, the trio of toothpicks (Leu2a, Z6a and Z5a) were stored in sterile straws. This 1:1:1 ratio of a trio of toothpicks with fungus, *Fusarium oxysporum* f. sp. *strigae* was denoted as Foxy T14.

The toothpick containing the fungus was delivered to the farmers, and they inoculated it in cooked and cooled pearled rice (ideal substrate to support the mycelial growth) to provide fresh on-farm inoculum of the fungal pathogen. Both the cooked rice and toothpick were placed in the sterile container and were shaken twice daily for three days. This technology was tested on 500 farms infested with *Striga* in Western Kenya. It has been reported that a drastic reduction in the infestation of *Striga* to the extent of 80% and 92% in the long and short seasons, respectively, subsequently enhanced the yield of maize by 56.5% and 42% in the long and short seasons, respectively. Here, the yield of maize grown in the short season declined due to drought. Additionally, it has been reported that the Foxy T14 lines had not produced toxins, conferring its non-toxic nature (Nzioki et al. 2016).

Management of *Parkinsonia aculeata* in Northern Australia. *P. aculeata* populations were massive in the Northern Australian region, possessing a serious threat to the ecosystem. So, to manage them, a bioherbicidal product (Di-Bak Parkinsonia®) comprising of three endophytic fungi viz., *Lasiodiplodia pseudotheobromae*, *Macrophomina phaseolina* and *Neoscytalidium novaehollandiae* was used. Di-Bak Parkinsonia is a capsule form of woody weed bioherbicide. It was successfully directed into the stem of the woody plants manually using an applicator device. The successful implant of the bioherbicide capsule resulted in the development of dieback symptoms. After a period of successful establishment, it progressed through the neighbouring untreated population, causing an enormous decline in the infestation vigour of *P. aculeata* (Galea 2021).

CELL-FREE CULTURE FILTRATES WITH HERBICIDAL VALUES

Cell-free culture filtrates have numerous advantages, which minimize the limitations attributed to conventional microbe-based products, especially on the shelf life and viability of the conidial suspension. Pathogens secrete a wide range of bioactive molecules and secondary metabolites. Such metabolites represent a large pool of compounds that can enhance crop growth and crop protection (Izurdiaga et al. 2023). Quereshi and Pandey (2007) extracted the cell-free culture extract of *Phoma* sp. FGCCW#54 which exhibited excellent herbicidal properties against *Parthenium hysterophorus*.

Similarly, cell-free culture filtrate of the fungal pathogen *Phoma herbarum* (FGCCPH#27) produced phytotoxic symptoms on *Parthenium hysterophorus* in shoot cut, seedling and detached leaf bioassays which revealed that the fungal pathogen has immense potential to produce several phytotoxic compounds with promising herbicidal values (Singh et al. 2013). The noxious weed *P. hysterophorus* can be biologically managed by exploiting the cell-free culture extract of *Alternaria macrospora* MKP1 and *Alternaria* sp. PMK2 (Kaur et al. 2016; Kaur & Aggarwal 2016). Singh and Pandey (2019a) reported that maximum disease ratings were observed in treating 21 days old cell-free culture filtrate of *Fusarium* sp. (FGCCW#16) at 100% concentration on *Parthenium hysterophorus*. Singh et al. (2010) stated that the cell-free culture filtrate of *Colletotrichum dematium* FGCC#20 produced severe phytotoxic symptoms in *P. hysterophorus*.

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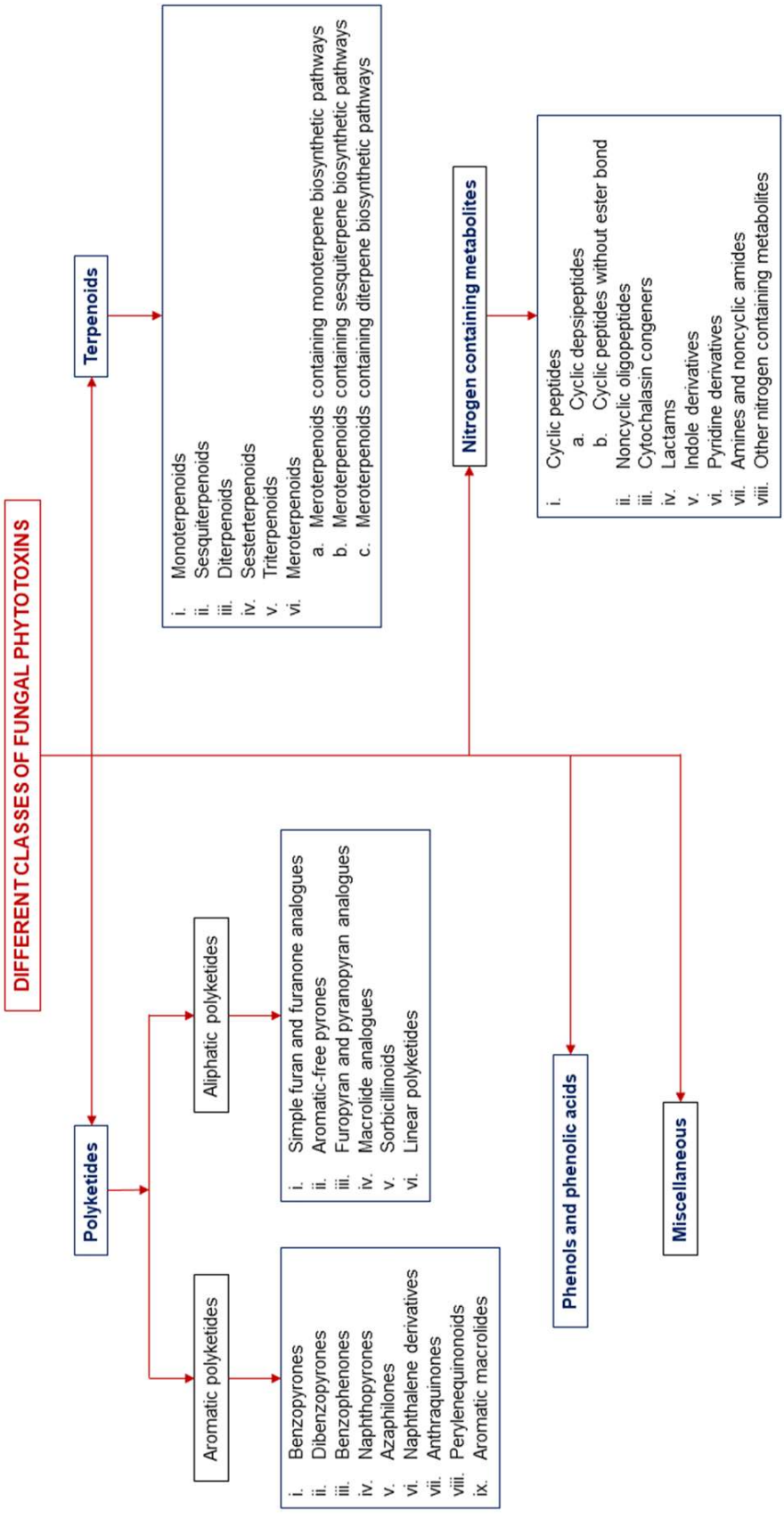

Figure 5. Different classes of fungal phytotoxins

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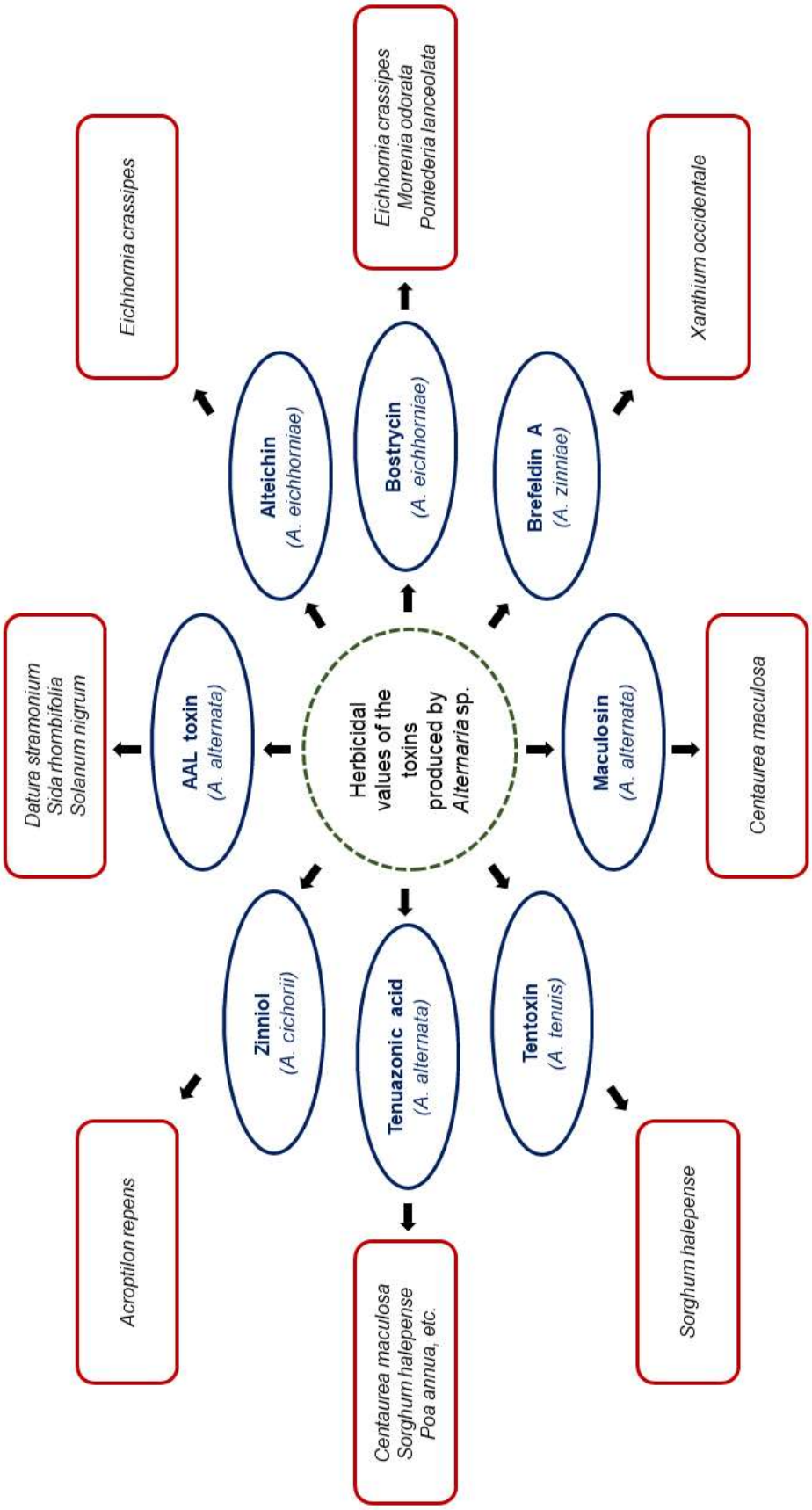

Figure 6. Mycotoxins produced by *Alternaria* sp. and its herbicidal values on different weed species

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Cell-free culture filtrate of the *Alternaria alternata* LC-110 and LC-104 strains induced phytotoxic symptoms on *Lantana camara* due to the toxic metabolites produced by the pathogen (Saxena & Pandey 2000). The 28-day-old cell-free culture extract of *Phoma herbarum* (FGCCW#18); 100% concentration resulted in maximum mortality and phytotoxic symptoms on *Xanthium strumarium* in the shoot cut and seedling bioassay (Singh & Pandey 2019b). *Helminthosporium* (FGCCW#53) pathogen cell-free culture filtrate exhibited excellent herbicidal potential against *Sida acuta,* causing severe phytotoxicity (Singh & Pandey 2021). The aqueous extract of *Macrophomina phaseolina* culture filtrate inhibited the seed germination of *Convolvulus arvensis*, *Malva neglecta* and *Sorghum halepense*. Moreover, the *in vitro* and *in vivo* studies also revealed that the aqueous extract of *Macrophomina phaseolina* culture filtrate produced phytotoxic damage to *Malva neglecta*, *Convolvulus arvensis*, *Poa pratensis* and *Sorghum halepense* (Theer et al. 2021).

SECONDARY METABOLITES

Plant pathogens synthesize and release various phytotoxins, which obstruct and intrude on plant metabolism, causing necrotrophic effects that might extend up to the mortality of plants. These phytotoxins possess a wide range of actions requiring a direct interface with a specified plant component like membrane or enzyme receptor, etc. (Vey et al. 2001). The absence and alteration of such receptors may not produce phytotoxic effects. So, the phytotoxins and their targets are indispensable factors affecting the pathogen's host range (Hoagland et al. 2007). These metabolites exhibit phytotoxicity at diverse stages of plant growth and development. Various classes of fungal phytotoxins are presented in Figure 5. Most of the phytotoxic fungal toxins belong to the classes of terpenoids (Bipolaroxin, Chenopodolin, Ophiobolins, Prehelminthosporol), polyketides (Ascochytine, De-*O*-methyldiaporthin, Monocerin, Putaminoxin), nitrogenous metabolites (Ascosonchine, Cytochalasins, Fumonisin B_1, Fusaric acid, β-nitropropionic acid, Tryptophol) and phenols and phenolic acids (Curvulin) (Xu et al. 2021; Bendejacq-Seychelles et al. 2024). The exploration for alternate ways of weed control resulted in the utilization of phytotoxic fungal toxins or secondary metabolites, and they were regarded as one of the most efficacious and eco-friendly approaches to weed management (Evidente 2023; Bendejacq-Seychelles et al. 2024). These phytotoxic fungal metabolites play a vital role in the biological control of weeds by causing chlorosis, necrosis, wilting, halting the germination of seeds and growth inhibition (Liu & Li 2004). These mycometabolites possess immense herbicidal values and can manage weeds through several mechanisms of action like altering the metabolic processes, triggering the production of ROS, ABA, ethylene, inhibiting germination and growth, etc (Radhakrishnan et al. 2018).

Phomentrioloxin, a mycotoxin isolated from the liquid culture of the fungal pathogen *Phomopsis* sp., exhibits immense mycoherbicide potential for managing *Carthamus lanatus*. The toxin causes necrotic spots on leaves when applied to the host and non-host plants at a concentration of 6.85 mM (Cimmino et al. 2012). Fungal pathogen *Phyllosticta cirsii* isolated from *Cirsium arvense* produces various phytotoxic metabolites with promising herbicidal properties when subjected to liquid culture. From the liquid culture of the pathogen, the compounds phyllostictines A-D were isolated. When tested on the host plant by leaf puncture assay, phyllostictine A was highly toxic, whereas phyllostictines B and D caused moderate phytotoxicity, and phyllostictine C had no effect (Evidente et al. 2008a).

Additionally, Evidente et al. (2008b) also reported that the further purification of the extract resulted in two toxins viz., phyllostoxin and phyllostin. When assayed on the punctured leaves of *Cirsium arvense*, phyllostoxin exhibited more phytotoxicity, causing necrotic symptoms, whereas phyllostin displayed no phytotoxicity. Likewise, several phytotoxic mycometabolites are involved in managing various weeds. Various toxins produced by different *Alternaria* sp. and their target weeds are illustrated in Figure 6. The metabolites of other mycopathogens, their target weeds and their mode of action are presented in Table 1.

NANOFORMULATIONS OF MYCOHERBICIDES

The controlled release of phytotoxic metabolites can be accomplished using nanoformulation technology. The toxin or metabolite can be coupled with a nanocarrier to protect it from degrada-

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Table 1. Fungal metabolites possessing promising herbicidal properties

Phytotoxin	Fungal pathogen	Target weed	Mode of action	Reference
Ascaulitoxin	*Ascochyta caulina*	*Chenopodium album*	potent growth inhibiting molecule	(Evidente et al. 1998; Cimmino et al. 2015)
Ascochytine	*Ascochyta hyalospora*	*Chenopodium album*	electrolyte leakage	(Venkatasubbaiah & Chilton 1992)
Ascosonchine	*Ascochyta sonchi*	*Sonchus arvensis, Salvia officinalis, Euphorbia helioscopia, etc.*	phytotoxicity producing necrotic circular lesions	(Evidente et al. 2004)
Bipolaroxin	*Bipolaris cynodontis*	*Cynodon dactylon, Sorghum halepense, etc.*	zonate lesions and flecking of leaves, elevated light intensities enhance the severity of symptoms	(Sugawara et al. 1985)
Cornexistin	*Peacilomyces variotii*	*Echinochloa crus-galli, Digitaria sanguinalis, Sorghum halepense, Solanum nigrum, etc.*	Inhibits the activity of amino transferase at higher concentrations only after incubating it in a plant cell extract	(Nakajima et al. 1991; Duke & Dayan 2011)
Chenopodolin	*Phoma chenopodicola*	*Cirsium arvense, Setaria viride* and *Mercurialis annua*	produces necrotic lesions	(Cimmino et al. 2013)
Curvulin	*Drechslera indica*	*Portulaca oleracea* and *Amaranthus spinosus*	produces necrotic symptoms	(Kenfield et al. 1989)
Cyperine	*Ascochyta cypericola*	*Cyperus* sp.	at higher concentrations, it inhibits the activity of protoporphyrinogen oxidase enzyme	(Stierle et al. 1991; Duke & Dayan 2011)
Cytochalasins (Z_1, Z_2, Z_3, B, F, T)	*Pyrenophora semeniperda*	*Bromus tectorum* and various genera of grasses	reduction in root growth	(Cimmino et al. 2015)
De-*O*-methyldiaporthin	*Drechslera siccans*	*Echinochloa crus-galli, Amaranthus spinosus* and *Digitaria* sp.	produces necrotic symptoms	(Hallock et al. 1988)
Fumonisin B_1	*Fusarium moniliforme*	*Datura stramonium*	disturbs the sphingolipid metabolism by inhibiting the activity of ceramide synthase enzyme	(Abbas et al. 1991)
Fusaric acid	*Fusarium nygamai*	*Striga hermonthica*	causes chlorosis, necrosis	(Capasso et al. 1996)
Hyalopyrone	*Ascochyta hyalospora*	*Chenopodium album, Sida rhombifolia, Senna obtusifolia, Ipomoea purpurea, Sorghum halepense, Agrostis, Ambrosia, Datura stramonium, etc*	electrolyte leakage	(Venkatasubbaiah & Chilton 1992)
Macrocidins A, B	*Phoma macrostoma*	Several broad-leaved weeds	bleaching of leaves and chlorosis	(Graupner et al. 2003)
Monocerin	*Exserohilum turcicum*	*Sorghum halepense* and *Cirsium arvenses*	Root necrosis and inhibits root elongation	(Robeson & Strobel 1982)
β-nitropropionic acid	*Septoria cirsii*	*Cirsium arvense*	Inhibits seed germination, root elongation subsequently followed by chlorosis and necrosis	(Hershenhorn et al. 1993)

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Table 1. to be continued

Phytotoxin	Fungal pathogen	Target weed	Mode of action	Reference
Ophiobolins (A, B,J, 6-*epi*-Ophiobolin, 3-Anhydro-6-*epi*-ophiobolin A)	*Drechslera sorghicola*	Ophiobolin A is highly phytotoxic to several monocots and dicots whereas 6-epi-ophiobolin exhibits reduced toxicity 3-Anhydro-6-*epi*-ophiobolin A is phytotoxic to *Setaria viridis* and *Diplotaxis erucoides* Ophiobolin B is highly toxic while ophiobolin J is slightly toxic to *Bromus* sp. and *Hordeum marinum*	inhibition of seed germination, electrolyte leakage, alters the permeability of cell membrane, causes necrotic lesions	(Evidente et al. 2006a) (Evidente et al. 2006b)
Prehelminthosporol	*Bipolaris* sp.	*Sorghum halepense*	produces necrotic spots and lesions	(Pena-Rodriguez et al. 1988)
Putaminoxin	*Phoma putaminum*	*Erigeron annuus, Mercurialis annua*, etc.	chlorosis and necrosis	(Evidente et al. 1995)
Pyrenolide A	*Ascochyta hyalospora*	*Chenopodium album*	electrolyte leakage	(Venkatasubbaiah & Chilton 1992)
trans-4-aminoproline	*Ascochyta caulina*	*Chenopodium rubrum*	produces large necrotic lesions	(Evidente et al. 2000)
Tryptophol	*Drechslera nodulosum*	*Eleusine indica*	produces necrotic lesions	(Sugawara & Strobel 1987)

tion (Hershenhorn et al. 2016). Namasivayam et al. (2015) reported that the coating of chitosan nanoparticles on the metabolite extracts of *Fusarium oxysporum* effectively controlled *Ninidam theenjan*. Nanoformulations of biochemical herbicides enhance the biocontrol efficacy due to the massive surface area exhibited by the nanoparticles, which in turn requires a lower volume of bioherbicide, thus intensifying the concentration in a smaller package at a lower cost (Pallavi et al. 2017).

CHALLENGES FOR THE DEVELOPMENT OF MYCOHERBICIDES

There are various challenges ahead for the successful development of a mycoherbicide. It may be due to technological, environmental, biological or commercial constraints (Auld et al. 2003). Technological constrictions like formulation type and mass production highly affect the development of mycoherbicide. With respect to the foliar application of fungal pathogens, the factors, viz., moisture, temperature, extent of leaf wetness, etc., significantly influence the germination and the ability to produce infection structures (Boyetchko et al. 2002). Since most pathogens require extended periods of leaf wetness or high humidity, i.e., dew period, to cause maximum infection, using mycoherbicides through foliar spray has been restricted to the irrigated areas. A major limitation attributed to the solid formulation is that they must wait for the suitable conditions required for the fungus to grow and induce infection vigorously. The weather factors such as temperature, relative humidity are the major constraints which severely influence the efficacy of mycoherbicides, as the fungal pathogens require a specific environmental condition to induce infections.

Regarding biological constraints, resistance and host variability are the prime limitations. To sort out the issues of host range and to augment the effectiveness of mycoherbicides, various efforts were made to amalgamate several host-specific pathogens for a single application. Accordingly, various efforts have been made to control closely related weeds by exploiting the fungal pathogens that possess a broad spectrum and extended host ranges (Rosskopf et al. 1999). In this multiple-pathogen strategy, two or more fungal pathogens were combined at ideal inoculum levels and applied over the target plants as pre- or post-emergence applications (Charudattan & Dinoor 2000). The practicability of this method has been proved in greenhouse con-

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ditions as well as in field conditions where seven grassy weeds were successfully controlled by the combined application of fungal pathogens viz., *Drechslera gigantea*, *Exserohilum longirostratum*, and *E. rostratum* as an emulsion (Chandramohan et al. 2000). Likewise, the fungal pathogens *Colletotrichum dematium*, *Phomopsis amaranthicola*, *Alternaria cassia* and *Fusarium udum* were combined to kill three different species of weeds (Chandramohan & Charudattan 2003).

Commercial constraints like the cost involved in the production of mycoherbicide and the market potential of mycoherbicides is too limited, so the companies are reluctant to come forward to develop mycoherbicidal products (Auld et al. 2003). From an economic perspective, a mycoherbicide controlling numerous closely related weeds (i.e., broad spectrum) would be encouraged (Duke 2024). The production costs of the mycoherbicides should be minimized and parallelly maintain the virulence of fungal pathogens with extended shelf life through efficient formulations and advanced application techniques (Golijan et al. 2023).

RISKS ASSOCIATED WITH MYCOHERBICIDES

The major risks associated with the utilization of mycoherbicides comprising of either fungal spores or their secondary metabolites are as follows.

Detrimental effects on non-target plants due to the introduction of non-native organisms. The mycoherbicidal formulations may also affect the main and subsidiary crops due to the introduction of non-native organisms. One such example was the release of the fungal pathogen *Puccinia melampodii* (isolated in Mexico) in Australia for the management of noxious and allergic weed *Parthenium hysterophorus* through an integrated approach even though the pathogen has the potential to sporulate on various sunflower and marigold cultivars (Evans 2000). However, over time, the Australian Quarantine and Plant Inspection Service reported that the pathogen, besides controlling the weed, caused serious damage to the non-target plants (Hoagland et al. 2007).

Mammalian and aquatic toxicity. Besides effectively controlling the target weeds, the toxins or metabolites produced by such pathogens might possess toxicity to humans, animals, etc. Foods and feedstuffs are habitually contaminated with the fungal toxicants consumed by humans as well as other animals, thus subsequently contracting diseases (Zain 2011). Aflatoxin B_1 and toxins derived from *Fusarium* sp. were also reported to cause potential damage to fish (Matejova et al. 2017).

CONCLUSION

Considering the hazardous effects of chemical herbicides on the natural environment and the rapid growth of organic agriculture systems, bioherbicides have been encouraged these days. Particularly, the use of fungal pathogens for managing weeds has attained remarkable progress in recent times with the development of various bioherbicidal products possessing different modes of action that perform well in various situations. A major drawback of utilizing fungal pathogens for managing weeds is that they are highly sensitive to environmental conditions, viz., temperature and relative humidity, which facilitate conidia germination and induce infection in the target weeds. To overcome these issues, the toxins produced by such fungal pathogens can be exploited so that they are highly specific only to the weed or group of weeds without negatively impacting the neighbouring crops and other life forms sustaining in that ecosystem. Further research has to be taken up for utilizing the mycometabolites for managing weeds, enhancing the efficacy of mycoherbicides by developing novel formulations and developing mycoherbicides possessing broad spectrum weed management properties for effectively managing the diverse weed biota. Moreover, advanced techniques like RNA interference, genomics and metabolomics can also be employed for effective weed management.

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