UDC 632.937.1:632.51
doi: 10.5937/AASer2355023G

Acta Agriculturae Serbica, 28 (55), 23–37, 2023

Publisher: Faculty of Agronomy Čačak

www.afc.kg.ac.rs

Weed biological control with fungi-based bioherbicides

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Received 24 November 2022; Accepted 6 April 2023

A B S T R A C T

Biological control refers to the use of living beneficial organisms as well as the products of their metabolism in pest control. Weed plants are indispensable companions of cultivated plants, in which they cause substantial damage. Organic food production, human health care and environmental preservation impose a need for the production and application of bioherbicides, particularly in organic systems of plant production. Plant pathogens have significant potential as biological agents in weed control. The aim of the present study was to indicate the most important properties of the weed biological control system, with particular emphasis on the use of fungi-based bioherbicides. According to the organism they suppress, biopesticides are classified into bioinsecticides, biofungicides, bioherbicides, etc. Weed control using plant pathogens can be performed in three ways, by classical, conservation and augmentative biological control. Bioherbicides were initially introduced to the market in 1980, and the majority of them were fungi-based bioherbicides. The most common fungi included in bioherbicides belong to the genera *Alternaria, Colletotrichum, Cercospora, Fusarium, Phomopsis, Phytophthora, Phoma, Puccinia*, etc. The studies, development and final commercialisation of fungi as biological control agents face many obstacles, ranging from basic biological facts to social and economic factors. There are also challenges in the production, formulation process, environmental friendliness, duration of herbicidal action, and expensive and time-consuming registration procedures. Considering the success in weed suppression with fungi-based bioherbicides, the global market is still dominated by chemical companies manufacturing synthetic herbicides, while there are no such products on the Serbian market yet.

Keywords: biological control, pathogens, fungi, weeds, bioherbicides, mycoherbicides.

И З В О Д

Под биолошком контролом подразумева се примена живих корисних организама, као и продуката њиховог метаболизма у контроли штеточина. Коровске биљке су неизоставни пратиоци гајених биљака, у којима проузрокују знатну штету. Производња здраве хране, брига о здрављу људске популације и очување животне средине намеће потребу за производњом и применом биохербицида, нарочито у органском систему биљне производње. Биљни патогени поседују значајан потенцијал као биолошки агенси у борби против корова. Циљ овога рада био је да укаже на најважније карактеристике биолошке контроле корова, са нагласком на употребу биохербицида на бази гљива. У зависности од организма који сузбијају, биопестициди се деле на биоинсектициде, биофунгициде, биохербициде и друге. Сузбијање корова применом биљних патогена може се вршити на три начина: класичном, конзервацијском и аугментативном биолошком контролом. Биохербициди су први пут уведени на тржиште 1980. године, а већина је на бази гљива. Најчешће гљиве које улазе у састав биохербицида припадају родовима *Alternaria, Colletotrichum, Cercospora, Fusarium, Phomopsis, Phytophthora, Phoma* и др. Истраживања, развој и финална комерцијализација гљива као биолошких агенаса за контролу суочавају се са бројним препрекама, почев од познавања основних биолошких знања до социо-економских фактора. Ту су и производне препреке, процес формулације, еколошка погодност, трајање хербицидног дејства и скупе и дуготрајне процедуре регистрације. С обзиром на успешност сузбијања корова применом биохербицида на бази гљива, светским тржиштем и даље доминирају хемијске компаније са производњом синтетичких хербицида, а у Србији и даље овакви препарати не постоје у промету.

Кључне речи: биолошка контрола, патогени, гљиве, корови, биохербициди, микохербициди.

1. Introduction

Biological control (biological suppression) is defined as the use of populations of parasitoids, predators, parasites, pathogens, antagonists, or competitors to regulate population densities of harmful organisms by reducing them, and thus reducing the damage they cause (Van Driesche and Bellows, 1996). Biological measures involve the suppression of weeds by the use of their natural enemies (predators and parasites of animal origin, and the use of viruses, bacteria and fungi) (Maceljski et al., 2002). It is believed that biological agents, also called "biorational pesticides", are successful because they are not single applied pesticides; once they are introduced into the environment, their permanent presence in the environment endangers unwanted plants (Petanović et al., 2000).

Although weed control is an indispensable operation in contemporary agricultural production, and although the use of herbicides is simple and effective, their application is not possible, desirable or sufficient in every situation. The excessive use of herbicides causes a number of adverse consequences, such as the occurrence of weed resistance, environmental pollution (residues in water and soil) and harmful effects on human and animal health (Barreto et al., 2000).

At the beginning of the 20th century, the biological control of harmful organisms was considered very unpromising, time consuming and ineffective. The reasons for choosing biological control over chemical control are: the effects of residues on human health, non-selectivity of pesticides, adverse side effects on non-target organisms, development of resistance in target pest species, high costs of synthesising new pesticides and obtaining permits for their use, effects on the environment, antipesticide legislation regulations and bans on the use of certain pesticides (Aračić, 2014). The history of biological weed control goes back to the end of the 18th century, while the earliest attempt was made as far back as 1795 with the introduction of the wild cochineal insect (*Dactylopius ceylonicus*) from Brazil to India in order to suppress the pear cactus (*Opuntia vulgaris*) (Maceljski, 2003). Plant pathogens have been used in weed control since the 1960s, and some of the first projects were the control of weed species of the genus *Rumex* in the USA, as well as *Rubus* spp. in Chile (Oehrens, 1977).

To be able to exhibit success, pathogens used in biological control must have certain properties, such as abundance, specificity, efficiency, changeability, ineradicability, ease of spread, self-regulation, and harmlessness for humans and animals (Petanović et al., 2000). Pathogens used in biological control affect weed species in various ways. Certain pathogens attach to the root system of plants and slow down their growth, while some infect the root, cut off the supply of water and nutrients and thus reduce leaf growth and development. Infections caused by some pathogens lead to necroses on the above-ground parts of plants, while others result in seed aging, reduced seed production, death of the whole plant and the like (Yandoc-Ables et al., 2006). Biological control has been accepted as a practical, safe, highly effective and ecologically friendly method of weed suppression, applicable in agroecological systems, without harmful effects on the health of consumers and producers (Charudattan, 2005).

In the United States and many other countries, the prescriptive use of plant pathogens as weed control agents is regarded as a pesticidal use and therefore these pathogens must be registered or approved as biopesticides by appropriate governmental agencies (Charudattan and Dinoor, 2000). The International Organisation for Biological Control (IOBC) promotes the development of biological control and its application in agricultural production. The IOBC coordinates biological control activities in six regions of the world (Africa, Asia and the Pacific, Eastern Europe, Western Europe and the Mediterranean, North and Central America, South America and the Caribbean), as well as in its working groups (Boller et al., 2006).

According to the organism they control, biopesticides are grouped into bioinsecticides, biofungicides, bioherbicides, etc. Bioherbicides are biological products used to control weed species through inundative or multiple applications, and are generally formulated on the basis of microbiological agents, namely fungi, and thus they are often called mycoherbicides (Ravlić and Baličević, 2014). The classification of biopesticides based on their active ingredients shows that there are approximately 2920 bacteria-based, 1658 fungi-based and 234 viruses-based biopesticides. Moreover, 227 bacteria-based and 169 fungi-based biopesticides are fungicides. The number of biopesticides in all categories has been significantly increasing (Palmieri et al., 2022).

Based on the relevant literature, the aim of this study was to point out the main characteristics of biological control methods for weeds, with particular emphasis on their suppression using fungi-based bioherbicides.

2. Properties of successful bioagents

According to Telkar et al. (2015), bioagents used in weed biological control should have the following properties:

a) *Host-specific*. Bioagents have to be able to live only on/in one species of the host; they should not infest and develop on other plants. They have to get through the starvation test, i.e. their response should be rather death than feeding upon other hosts.

b) *Hardiness*. Bioagents have to get rid of their own predators and parasites. They should also be capable of enduring prolonged or short-term starvation when the weed species they are intended for are scarce.

c) *Feeding habit.* Better weed suppression is accomplished if bioagents infest flowers and seeds of weeds, or if they feed on stems rather than on roots and leaves. On the other hand, bioagents attacking and feeding on roots are more successful in the control of perennial weed species.

d) *Ease of multiplication*. Natural multiplication of bioagents should be high and easy. It is extremely significant for pests and plants that compete with them.

e) *Types of classical bioagents*. There are two categories of these agents: specific and non-specific. The first one infests one or two specific weed species, while the second one can attack different weeds. Insects, microorganisms causing diseases and plants competing with bioagents belong to specific bioagents. On the other hand, non-specific bioagents include some fish species, like carp, snails, mites (Telkar et al., 2015).

3. Advantages and conditions for the application of biological agents

As already mentioned above, bioagents should be able to live only on/in one species of the host; they should not infest and develop on other plants beneficial to man. They have to get through the starvation test, i.e. their response to food shortage should be rather death than feeding upon other hosts. There are many steps from research to commercialisation in the process of introduction of biological control agents (BCAs): isolation of BCAs from the environment; preparation of studies with the aim of generating knowledge within several fields (ecology, physiology and taxonomy of potential BCA fungi); performance of laboratory/field tests that provide the identification of potential antagonists, virulence and ecologically suitable strains; doses and rates of mortality; suppression and the time of suppression; study of the economic justification and large-scale production of a stable inoculum; development of the application strategy that greatly affects BCA efficiency; risk assessment as a basis for the registration process that must prove that the use of BCAs is safe for humans and other non-target organisms; training processes in which a BCA is integrated into a unique protection programme that is easy to manage (http://www.agroservis.rs/biopesticidi-u-svetu).

The application of microbial technology is relatively simple. Once introduced into the plant community, they continue to maintain themselves. Their abundance provides a wide selection of particularly specialised ones. They are not harmful to humans. They never have a completely eradicative effect. They do not completely destroy the plant species, that is, the host plant, which enables regeneration of the association (Petanović et al., 2000).

Some of the potential advantages and disadvantages of BCAs over chemical agents in plant disease control are: very environmentally friendly, non-persistent, a lower tendency to resistance; however, they exhibit a lower level of control, cannot provide long-term control, can undergo mutations and variability, cannot be applied on large areas (http://www.agroservis.rs/biopesticidi-u-svetu).

The introduction of microorganisms, plant pathogens, requires a cautious approach and careful handling. The advantages of microbial agents include: 1) susceptibility to chemical agents (wetting agents, fungicides, insecticides, herbicides, mineral liquid fertilizers), 2) abundance and diversity, 3) specificity, 4) efficacy, 5) variability/changeability, 6) ineradicability, 7) ease of spread and self-regulation, 8) harmlessness to humans and animals (Petanović et al., 2000).

4. Limitations

There are some limitations of weed biological control by plant pathogens: 1) there is almost no commercial interest – markets for biological agents for weed control are insignificant and therefore there is no interest in industrial production; 2) it is very difficult and complex to produce the inoculum of prolonged action for a wide range of use and therefore quite a few potential agents have been given up completely. This technology could be boosted if a bioherbicide that can control closely associated weeds even if they occur in various cultivated plants and different regions is developed. The production of a bioherbicide that could be used in different cultivated plants and could control a number of weed species can be profitable and therefore could arouse interest in this technology. Moreover, there is an idea to increase the efficiency and suitability of bioherbicidal agents by combining a number of pathogens specific to a certain host into a single application. In this strategy with different pathogens, three or more pathogens are mixed at the optimum inoculum levels and applied pre- and post-emergence to control weeds. More should be done on the characterization of genes that can be valuable for the improvement of the effectiveness of bioherbicidal pathogens. Insufficient support is one of crucial limitations to classical weed biological control by plant pathogens. Many funding institutions and agencies are unwilling to provide funds because it seems that classical biological control and the whole process of finding and applying plant pathogens is too slow, too time-consuming and unprofitable. Nevertheless, the successful cases and profits from them show that this control is one of the best alternatives (Charudattan and Dinoor, 2000).

More funds are allocated for the development of chemical pesticides than for studying and developing fungal BCAs. This is due to the fact that mycopesticides often have a narrow range of hosts and because the results obtained in field trials showed that they exhibited inconsistent or poor control. This resulted in the development of wider spectrum biopesticides. The benefit of intense selectivity is lost if it is determined that fungi have a broader spectrum of biological action, while the environmental advantage may be wasted for the sake of wide-spectrum control (Butt and Copping, 2000).

5. Technical issues

Figure 1 presents the strategic framework for the evaluation and development of mycoherbicides. In order to develop efficient fungal biological control agents, several technical problems have to be solved (Butt and Copping, 2000):

1) **Speed of action.** Fungal BCAs are often disapproved of because of their slow action, due to which crops are protected to some degree, partially. Determinants of virulence in pathogens should be recognised and used when selecting strains and in quality control.

2) **Greater ecological fitness.** Although most fungi have good performance in the laboratory, their performance in the field is often poor. Fungal BCAs have to be prepared for field conditions, i.e. only strains that tolerate various factors of climate, soil and antagonists should be selected;

3) **Production.** Production costs have to be decreased so that the costs of the end product are not higher than the costs of conventional pesticides. Virulence and ecological fitness must be maintained or even enhanced. Packaging and handling of products must not be complicated. The shelf life of products has to be adequate for the user;

4) **Virulence.** Fungi tend to lose virulence or antagonistic activity on cultivation media. Cultural conditions that maintain virulence with equal production costs should be established;

5) **Formulation.** An efficient formulation is of crucial importance for obtaining performances in fields equal to those in laboratories. Therefore, more efficient components of formulations have to be searched for. It is also very important that these components be well suited to other BCAs that can be applied simultaneously with the fungal BCA;

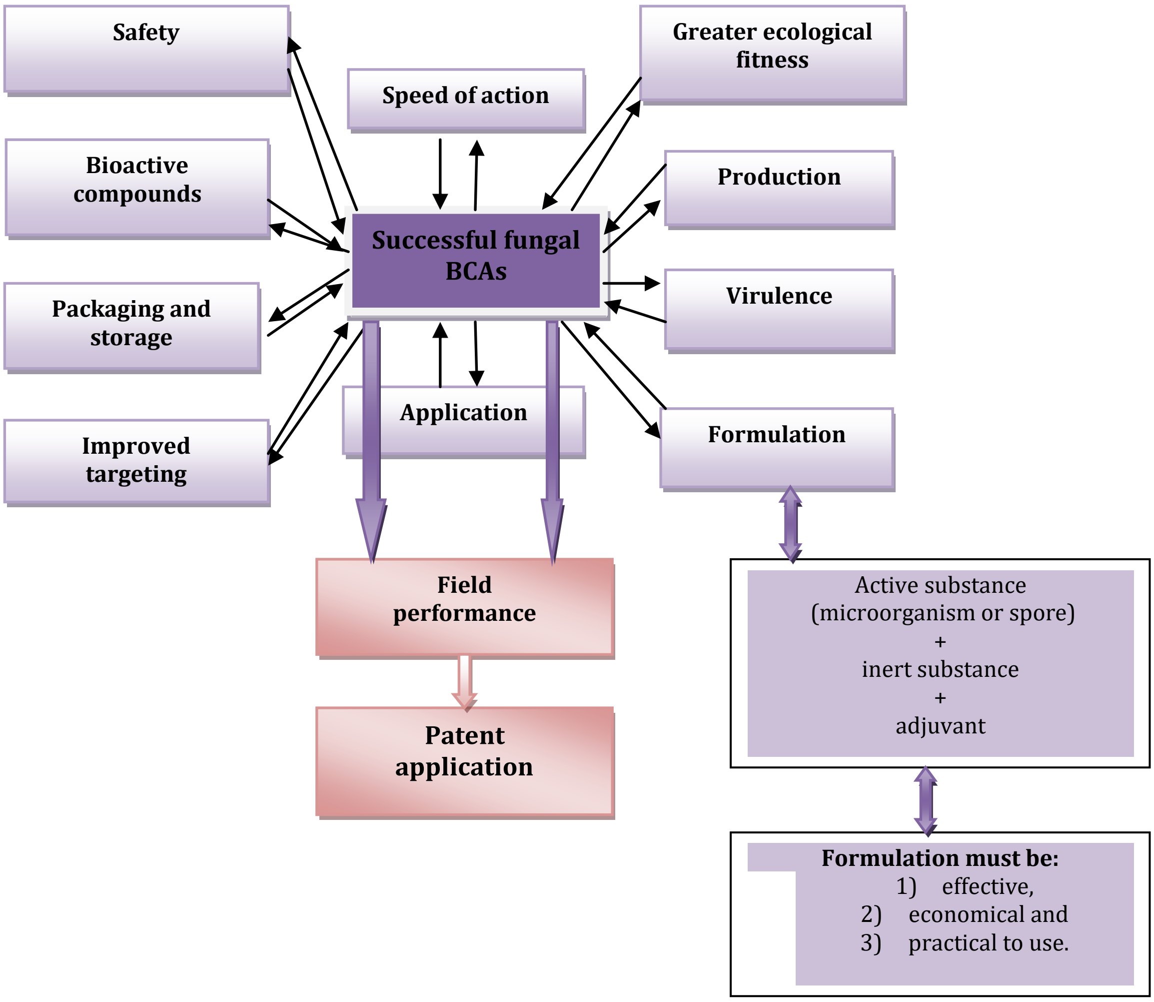

Figure 1. Strategic framework for the evaluation and develepment of mycoherbicides

6) **Application**. It is necessary to apply BCA products using standard equipment or the one with certain specific requirements for the application.

7) **Improved targeting**. It is necessary to determine precisely where money and time will be spent for BCAs in the control of pests, weeds and diseases.

8) **Packaging and storage.** Neither farmers nor suppliers will use or distribute new BCA products if the expiration date packing and storage requirements differ much from those of classical chemicals. For instance, if conventional chemicals do not need to be refrigerated and their corresponding BCAs need to be;

9) **Bioactive compounds.** It is well known that a lot of fungi produce biologically active secondary metabolites. A number of these metabolites are extremely toxic. This is a significant problem with all fungal BCAs, because their existence would endanger health. Therefore, certain studies have to be performed in order to: a) screen for the identification of bioactive compounds in fungal BCAs, b) establish the function of these compounds, and c) determine a mechanism of action of these compounds;

10) **Safety**. Safety is a foremost interest for all products indented for use in the protection of cultivated plants. Therefore, additional research is necessary in order to establish any risk arising from the application of fungal BCAs. Attention should be paid to allergic traits, risk of toxic metabolites and genetic recombination and dislocation of natural strains, and impact on biodiversity, such as effects on non-target entities.

6. Methods of biological control

The application of biological control in general, and biological control against weeds in particular, is achieved through the following approaches:

a) Classical biological control involves protection against introduced weed species with allochthonous organisms, that is, organisms from the regions of weed origin. It is generally applied for permanent protection against perennial weed species in ruderal habitats, pastures or channels (Petanović et al., 2000). For successful biological control, it is necessary to determine whether the pathogen is harmful to the target weed species that needs to be suppressed, but at the same time it must be harmless to other non-target plant species (host specificity testing/host range testing). Furthermore, it has to be adapted to the ecological system into which it was introduced, cause damage to the target weed species and reduce its population

(Froude, 2002). This approach is by far the most successful and the most frequently used method. Unfortunately, there are also some disadvantages of this method, because once a pathogen is introduced into a new region, there is danger that, due to the lack of native, natural enemies, its spread will become uncontrolled and dangerous for the environment into which it has been introduced. Until 1996, about 1150 classical biological programmes were implemented, i.e. 365 natural enemies were released for the control of 133 target weed species (Julien and Grifiths, 1998).

b) **Augmentative biological control** (Lat. *augmentatio* = the act of making bigger, the process of increasing) involves the mass propagation and periodic release of exotic or autochthonous natural enemies. It is used for the temporary suppression of native or introduced weed species.

c) **Conservation biological control** (Lat. *conservatio* = preservation, keeping) – agroecosystems are organised in such a way as to maximise the effect of autochthonous natural enemies (Petanović et al., 2000). This approach involves the preservation and (or) creation of favourable conditions for autochthonous (native) natural enemies, that is, manipulation of already existing autochthonous organisms in the environment. This concept starts from the assumption that natural enemies already existing in the environment have competitive advantage, e.g. large reproduction, and thus the target weed is successfully suppressed. For the time being, this approach has no major significance in the biological control of weeds (Aračić, 2014).

7. Bioherbicides – Types of bioherbicides and currently marketed products

The first bioherbicides occurred on the market in 1980. Since then, several biopesticides, including bioinsecticides, biobactericides, biofungicides, and bionematicides, have been introduced into the world market, but the participation of bioherbicides is still below 10% of all marketed biopesticides (Hintz, 2007). Resistance to classical types of herbicides has particularly contributed to the development of bioherbicides. Resistance to different herbicide classes has occurred in numerous plant species throughout the world, particularly if and where monoculture, monoherbicide and minimum tillage are widely practised (Janjić et al., 2007).

A great interest in the exploitation of fungi for pest, weed and disease control has been confirmed by numerous commercial products that are already available, as well as by many developmental projects. The study, development and final commercialisation of fungi as biological control agents are constantly faced with numerous obstacles, starting from basic biological knowledge to socio-economic factors. Significant advances have been made in certain areas, but it is important to integrate them with newly gained information (http://www.agroservis.rs/biopesticidi-u-svetu).

Better results in biological control are usually obtained with weeds that have a lower potential for induced resistance, that is, defence against all types of stress. A bioagent should have certain properties to be successful, but the weed plant should also have certain traits in order that the bioagent can be successful (Petanović et al., 2000):

1) it has to be preferential for phytophages or pathogens in comparison to other plants of the spontaneous vegetation,
2) the weed species has to be particularly attractive as a host plant for phytophagous species and pathogens,
3) it should be genetically uniform throughout the region, that is, it should not form biotypes with different nutritional values of different other traits.

The formulation of bioherbicides consists of an active ingredient (microorganism or spore), a carrier (inert matter) and an adjuvant. According to the available scientific literature, the activity of weed killers was enhanced by the formulation of microbial metabolites (Sica et al., 2016; Bastos et al., 2017). An adjuvant can contain nutrients of chemicals that help a pathogen to survive or protect it from adverse environmental conditions (Hynes and Boyetchko, 2006). Adjuvants can also aid in host infection. According to Weaver et al. (2009), the hydrophilic-lipophilic balance (HLB) value of an adjuvant can result in a higher bioactivity of a bioherbicide. It can also enhance abilities of the formulation to change. The application of a formulation with high HLB values improves water absorption by a cuticle, and thus increases the transmittance of hydrophilic herbicides onto the leaves. As a result, the herbicidal rate of diffusion in a constant concentration gradient is higher (Bastos et al., 2017). The positive result of formulation 06, with a high HLB, might have been due to the high concentration of palm oil (Todero et al., 2018). Vegetable oils dissolve fats that are contained by the cuticle. Once these obstacles are eliminated, the penetration of the hydrophilic herbicides by the cuticle is greater (Vargas and Scherer Roman, 2006).

The main task of the formulation is to ensure that the pathogen remains viable, virulent and with sufficient inoculum potential to be effective in the field. An effective formulation has to be efficient, economical and practical to use (Ash, 2010). The main drawback of bioherbicides is their low herbicidal activity (Varejão et al., 2013). This disadvantage can be overcome by synthetic modifications (Sica et al., 2016) or by the use of an appropriate adjuvant mixture in a formulation to enhance herbicidal activity (Rana and Rana, 2016).

As the result of their very different nature, fungi-based biopesticides have different mechanisms of action. Competition, mycoparasitism and metabolite production are the most common mechanisms of action. Some fungi can express all three mechanisms (Golijan and Sečanski, 2022).

Until 2012, seven bioherbicides were registered in the USA, six in Canada, and one in both Ukraine and Japan (Bailey, 2014). Until 2016, there were nine fungi-based bioherbicides, three bacteria-based bioherbicides and only one plant extract-based bioherbicide on the world market (Cordeau et al., 2016). Six commercial bioherbicides based on essential oils and/or their compounds were registered and were available in the USA until 2020 (Verdeguer et al., 2020).

8. Fungi-based bioherbicides

The majority of bioherbicides obtainable on the market are based on fungi. The most common fungi included into the bioherbicides are: *Alternaria destruens, A. sonchi, A. alternata, A. helianthi, Colletotrichum gloeosporioides, C. truncatum, C. coccodes, Cercospora rodmanii, Fusarium oxysporum, F. nygamai, F. tumidum, Mycelia sterile, Phomopsis amaranthicola, Phytophthora palmivora, Phyllosticta cirsii, Phoma destructiva, P. hedericola, P. nebulosa P. herbarum, P. macrostoma, Puccinia thlaspeos, Sclerotinia minor, Verticillium albo-atrum* (Vuković and Šunjka, 2021).

The simple use of the fungus *Fusarium oxysporum* Schlecht against the Indian fig opuntia (*Opuntia ficus-indica* (L.) Mill.) was the initial project with biological herbicides implemented in 1940. Then, in the 1950s, the parasitic weed dodder was suppressed with *Alternaria cuscutacidae* Rudakov (Pacanoski, 2015). In the late 1960s, an elaborate programme was set up to detect pathogens of *Rumex* spp. in the United States (Inman, 1971), as well as pathogens of *Rubus* spp. in Chile to control weeds (Oehrens, 1977). In North America, 18 species of fungi were considered potential biological control agents of weeds (Charudattan, 1985). Mycoherbicides were discovered in the mid-1970s and they are considered to be the first bioherbicides. Since then, many bioherbicides have been developed, registered and obtainable on the world market (Zeng, 2020). Devine, the first bioherbicide registered, was developed in the Abbott Laboratories and produced from a facultative fungus *Phytophthora palmivora* Butl. This fungus causes root rot of latexplant and can be effective for a long time because it remains in the soil as a saprophyte (TeBeest, 1990).

Triolet et al. (2019) analysed studies conducted over a 45-year period (1973–2018) related to fungi and natural fungal molecules and their related target weeds, and found that the most broadly studied genera were: *Colletotrichum, Alternaria, Puccinia, Phoma* and *Fusarium*. Half of the scientific articles were related to these genera: 38, 36, 30, 20 and 17 articles referenced to *Colletotrichum, Alternaria, Puccinia, Phoma* and *Fusarium*, respectively.

The first bioherbicides were produced and commercialised in the USA in the 1980s. Some of these bioherbicides are: Devine®, Collego®, Casst®, Dr. BioSedge®, BioMal®, Stumpout®, Biochon®, Camperico®, Woad Warrior®, Smolder®, and Myco-Tech® (Aneja et al., 2013). At present, there are more than 200 plant pathogens on the waitlist to be commercialised as bioherbicides (Pacanoski, 2015). Table 1 presents some fungi-based bioherbicides and their target weeds, while Table 2 shows commercial products available on the markets.

Alternaria destruens L. Simmons strain 059 was isolated from a parasitic plant swamp dodder (*Cuscuta gronovii*) in 1986 (Bewick et al., 1987). The use of this fungus as a bioherbicide was patented in 1990 and registered under the name Smolder™ (Bewick et al., 2000). It is used to suppress species of the genus *Cuscuta (C. gronovii*, *C. indecora*, *C. planiflora,* etc.). It is produced by fermentation. Pathogenesis is the basic mechanism of action of this bioherbicide. The isolate of *Alternaria destruens* 059 is produced in the form of granules (GR) and a wettable powder (WP). The product was commercialised and first used in the USA in 2005. It is approved for use in organic agriculture (Vuković and Šunjka, 2021).

The bioherbicide Devine® containing the *Phytophthora palmivora* Butler strain MVW was registered as a bioherbicide and commercialised in 1981 to be used in citrus crops for the control of the weed latexplant (*Morrenia odorata*) (Kenney, 1986).

Sauerborn et al. (2007) asserted that species of the genus *Fusarium* as soil-borne pathogens may be suitable for bioherbicides in the control of parasitic flowering plants. Six *Fusarium* species (*F. arthrosporioides*, *F. nygamai*, *F. oxysporum*, *F. oxysporum* f.sp. *orthoceras*, *F. semitectum* var. *majus*, *F. solani*) showed significant disease development on the selected species of the genus *Orobanche. F. oxysporum,* a potential mycoherbicide, used in the control of parasitic witchweed plants, affected their emergence by 81.8%–94.3%, depending on weed species (Marley et al., 2005). Some mechanism of action of *Fusarium oxysporum* includes disease induction, necrosis, ethylene production, inhibition of seed germination, and infection of seed coat and endosperm (Ray and Vijayachandran, 2013).

Cercospora rodmanii was isolated from water-hyacinth (*Pontederia crassipes*) in Florida and is used to suppress plants of this species. The basic mechanism of action is pathogenesis. It causes small (2–4 mm in diameter) necrotic spots on the leaf and the petiole. It can spread quickly and easily through water causing large areas of weed plants to become brown and necrotic (Vuković and Šunjka, 2021).

The bioherbicide *Phoma macrostoma* strain 94-44B was derived from the fungus *Phoma macrostoma*. This bioherbicide was developed to suppress dicotyledonous weeds in turfgrass (Bailey et al., 2011; Bailey, 2014). The fungus is known for its attacking, colonising and passing into the root system of weed plants, where it develops its mycelia blocking the intake of nutrients.

The fungus *Colletotrichum gloeosporioides* was isolated from Virgina jointvetch (*Aeschynomene virginica*) and it is used to control plants of this genus in the soya bean and rice crops. Pathogenesis is its mechanism of action. When applied to weed plants, the fungus penetrates into the plant cuticle, causing dying of plants. It is produced through the process of fermentation, in the form of aqueous suspension of spores, powder (DP) or water-dispersible granules (WG) (Vuković and Šunjka, 2021). BioMal®, a bioherbicide that is no longer available, composed of *C. gloeosporioides* f. sp. *malvae* strain ATCC 20767, was registered in Canada in 1992. Its target weed was low mallow (*Malva pusilla*) usually in wheat, lentil and flax (Mortensen and Makowski, 1989; Boyetchko et al., 2007). *Colletotrichum coccodes* strain DAOM 183088 is considered a potential bioherbicide for velvetleaf (*Abutilon theophrasti*), one of the most detrimental weeds to maize and soya bean in the USA (Dauch, 2006). Collego®, renamed LockDown® in 2006, a bioherbicide derived from *C. gloeosporioides* f. sp. *aeschynomene* strain ATCC (American Type Culture Collection) 20358, was registered and commercialised in the USA in 1982 to control Virgina jointvetch (Bowers, 1982, 1986).

The fungus *Phomopsis amaranthicola* has originally been isolated from redroot pigweed (*Amaranthus retroflexus*) in Florida. It is produced through fermentation. It suppresses the majority of plant species of the genus *Amaranthus.* Pathogenesis is its mechanism of action. The pathogen forms foliar lesions that cause defoliation. The product based on this fungus is allowed for use in organic farming (Vuković and Šunjka, 2021).

It has been established that *Puccinia* species is effective in suppressing different weed species such as groundsel, creeping thistle and woad (Müller-Schärer and Frantzen, 1996; Bailey, 2014; Berner et al., 2015). *Puccinia thlaspeos* was discovered in Idaho, USA in 1979, and has since spread throughout the United States. It was produced on the living plant of woad, and it is used for its control on non-agricultural lands, plot borders, canals, but its application is not allowed in cultivated crops. It is produced in powder form and applied directly to the ground and young plants in April and May when new plants start growing, or it is applied foliarly (Vuković and Šunjka, 2021). *Puccinia thlaspeos* could be a potential and effective biocontrol agent for woad control (Lovic et al., 1988). As a result of this, the bioherbicide Woad Warrior® was registered in the United States in 2002 (Stirk et al., 2006).

The fungus *Sclerotinia minor* Jagger strain IMI 344141 has been registered as a biological herbicide named Sarritor to control dicotyledonous weeds in Canadian turfgrass (Ciotola et al., 1991; Brière et al., 1992). The strain IMI 344141 was isolated from a lettuce field in Canada in 1983. It is used to control dandelion (*Taraxacum officinale*). It is used on lawns, golf courses and parks. This bioherbicide is produced by fermentation. The mechanism of action is based on the effects of oxalic acid that is exuded by *S. minor*, and is toxic to dandelion plants. It is permitted for use in organic farming (Vuković and Šunjka, 2021).

The fungus *Chondrostereum purpureum* (Fr.) Pouz. controls the shoots of black cherry and Canadian poplar. The *C. purpureum* strain PFC 2139 was registered and marketed under the name Chontrol® Pastes in Canada and the USA in 2004 (Bailey et al., 2010).

Table 1.
Fungi-based bioherbicides and their target weeds.

Fungi	Target weeds	References
Colletotrichum gloesporioides	*Leguminosae, Malvaceae, Convolvulaceae* (C. spp.)	Daniel et al. (1973), Mortensen and Makowski (1997)
C. coccodes, F. lateritium	*Abutilon theophrasti* Medik.	Walker (1981), Hodgson et al. (1988)
Ascochyta caulina, Cercospora chenopodii, C. dubia	*Chenopodium album* L.	Scheepens and van Zon (1982)
Alternaria cassiae	*Senna obtusifolia* (L.) H. S. Irwin and Barneby, *S. occidentalis* (L.) Link, *Crotalaria spectabilis* Roth	Walker (1983), Charudattan et al. (1986), Boyette (1988)
Septoria tritici f. sp. *avenae*	*Avena fatua* L.	Madariaga and Scharen (1985)
Sclerotinia sclerotiorum	Multiple species	Brosten and Sands (1986)
Amphobotrys ricini	*Euphorbiaceae*	Whitney and Taber (1986), Holcomb et al. (1989)
Cochliobolus lunatus	*Echinochloa crus-galli* (L.) P. Beauv	Scheepens (1987)
Pseudocercospora nigricans	*S. obtusifolia*	Hofmeister and Charudattan (1987)
Colletotrichum dematium	*Leguminosae*	Cardina et al. (1988)
Colletotrichum orbiculare	*X. spinosum*	Auld et al. (1988)
Dichotomophthora indica, D. portulacea	*Portulaca oleracea* L.	Evans and Ellison (1988)
P. grisea	*E. indica*	Figliola et al. (1988)
Colletotrichum truncatum	*Sesbania exaltata* (Raf.) Rydb. ex A.W.Hill	Boyette (1991)
S. minor	*T. officinale, Trifolium repens* L., *Plantago minor* Garsault	Riddle et al. (1991)
Exserohilum monoceras	*Echinochloa* spp.	Zhang and Watson (1997)
Alternaria destruens	*Cuscuta* spp.	Simmons (1998)
P. herbarum	*Taraxacum officinale* (L.) Weber ex F.H. Wigg	Neumann and Boland (1999)
Alternaria helianthi	*Xanthium strumarium* L.	Abbas et al. (2004)
Alternaria eichhorniae	*Eichhornia crassipes* (Mart.) Solms	Shabana (2005)
Myrothecium verrucaria	*S. obtusifolia, Portulaca* spp., *Euphorbia* spp.	Boyette et al. (2007)
Bipolaris setariae	*Eleusine indica* (L.) Gaertner	Hoagland et al. (2007)
Cercospora caricis	*Cyperus esculentus* L.	Hoagland et al. (2007)
C. graminicola	*Gramineae*	Hoagland et al. (2007)

F. lateritium	*Ambrosia trifida* L.	Hoagland et al. (2007)
Phomopsis convolvulus	*Convolvulus arvensis* L.	Hoagland et al. (2007)
Phyllachora cyperi	*Cyperus rotundus* L.	Hoagland et al. (2007)
Pyricularia sp.	*Digitaria sanguinalis* (L.) Scop.	Hoagland et al. (2007)
F. oxysporum	*Phelipanche ramosa* (L.) Pomel	Kohlschmid et al. (2009)
Ascochyta agropyrina	*Chenopodium album* L., *Cirsium arvense* (L.) Scop., *Mercurialis annua* L., *Sonchus oleraceus* L., *Setaria virdis* (L.) P.Beauv.	Cimmino et al. (2013a)
Phoma chenopodicola	*C. album, Cirsium arvense* (L.) Scop., *Setaria viridis* (L.) P. Beauv., *Mercurialis annua* L.	Cimmino et al. (2013a)
Phoma herbarum	*P. hysterophorus, Lantana camara* L., *Hyptis suaveolens* (L.) Piot., *Sida acuta* Burm.f.	Kalam et al. (2014)
Puccinia sp	*Senecio vulgaris, Cirsium arvense, Isatis tinctoria*	Müller-Schärer and Frantzen (1996), Bailey (2014), Berner et al. (2015)
Diaporthe gulyae	*Papaver rhoes* L., *Ecballium elaterium* (L.) A.Rich., *Urtica dioica* L., *Hedysarum coronarium* L.	Andolfi et al. (2015)
P. macrostoma	*T. officinale*	Smith et al. (2015)
Bipolaris sorghicola	*Sorghum halepense*	Telkar et al. (2015)
Uromyces rumicis	*Rumex* spp.	Telkar et al. (2015)
Sclerotinia sp.	*Orobanche cernua*	Telkar et al. (2015)
Septoria cirsii	*Cirsium arvense*	Telkar et al. (2015)
Puccina chondrillina	*Chondrilla juncea*	Telkar et al. (2015)
Myrothecium roridum	*Eichhornia crassipes* (Mart.) Solms	Piyaboon et al. (2016)
Fusarium fujikuroi	*Cucumis sativus* L., *Sorghum bicolor* (L.) Moench.	Daniel et al. (2018)
Lasiodiplodia pseudotheobromae	*Solanum lycopersicum* L., *Amaranthus hybridus* L., *E. crus-galli*	Adetunji et al. (2018)
Sclerotium rolfsii	*Solidago canadensis* L.	Zhang et al. (2019)
Cercospora rodmanii	*Eichhornia crassipes*	Vuković and Šunjka (2021)
Colletotrichum gloeosporioides	*Aeschynomene virginica*	Vuković and Šunjka (2021)
Phomopsis amaranthicola	*Amaranthus* spp.	Vuković and Šunjka (2021)
Puccinia thlaspeos	*Isatis tinctoria*	Vuković and Šunjka (2021)
Sclerotinia minor	*Taraxacum officinale*	Vuković and Šunjka (2021)

Table 2.
Commercialised fungi-based bioherbicides and their target weeds.

Fungi	**Target Weeds**	**References**
A. cassia (commercialised Casst™)	*Cassia obtusifolia* L., *C. occidentalis* L., *C. spectabilis* DC.	Charudattan et al. (1986)
P. canaliculata (commercialised Dr. BioSedge®)	*Cyperus esculentus L.*	Phatak (1992)
Cephalospprium diospyri (commercialised Oklahoma)	*Diospyras virginiana* L.	Julien and Griffiths (1998)
*Cylindrobasidium leave (*commercialised Stumpout™)	*Poa annua* L., *A. mearnsii* (De Wild) and *A. pycnantha* (Benth.)	Shamoun and Hintz (1998)
Alternaria destruens (commercialised Smolder™)	*Cuscuta* spp.	Bewick et al. (2000)
Colletotrichum gloeosporioides aeschynomene (commercialised-Collego™)	*Aeschynomene virginica* L.	Tateno (2000)
Colletotrichum coccodes (commercialised-Velgo®)	*Abutilon theophrasti*	Butt (2000)
*Cercospora rodmanii (*commercialised 'ABG 5003')	*Eichhornia crassipes*	Charudattan (2001)

C. purpureum (commercialised-BioChon™)	*Prunus serotina*	Stewart-Wade et al. (2002)
Chondrostereum purpureum (Fr.) Pouz (commercialised Myco-Tech™ paste)	Deciduous tree species in forests	Charudattan (2005)
Puccinia thlaspeos (commercialised Woad Warrior®)	*Isatis tinctoria* L.	Stirk et al. (2006)
Phytophthora palmivora (commercialised- Devine™)	*Morrenia odorata* (Hook. &Arn.) Lindl.	Hintz (2007)
Colletotrichum gloeosporioides (commercialised-Hakak)	*Hakea sericea* Schrad.&J.C.Wendl.)	Hintz (2007)
C.purpureum (commercialised Chontrol™ = Ecoclear™)	Hardwoods in forests	Bailey et al. (2010)
Colletotrichum gloeosporioides malvae (Commercialised-BioMal®)	*Malva pusilla* Sm.	Bailey and Falk (2011)
Phoma macrostoma (commercialised-Phoma)	*Reynoutria japonica* Houtt.	Pest Management Regulatory Agency (2013)
Acremonium diospyri	*Diospyros virginiana* L.	Aneja et al. (2013)
S. minor (commercialised Sarritor®)	*Taraxacum officinale (L.)*	Aneja et al. (2013)
Alternaria destruens (Field evaluation- Smolder)	*Cuscuta* spp.	Bailey (2014)
Colletotrichum gloesporiodes f. sp *cuscutae* (commercialised Luboa-2)	*Cuscuta* spp.	Telkar et al. (2015)

The use of mycoherbicides is going to increase permanently due to the return on investments. Every dollar spent on invasive plant biological control has a return on investment of 23 dollars (Queensland Government, 2019). Thus, the benefit-cost ratio is 23 to 1. Cullen (1985) reported that the project implemented for skeletonweed biocontrol resulted in benefits to users in the amount of 100:1 or 200:1.

10. Phytotoxins produced by fungi phytopathogenic for weeds

Fungi inhibit the growth of weed plants by various mechanisms. Little work has been done to make clear the physiological aspects of weed × fungi interactions when treatments with mycoherbicides were applied. Certain studies emphasised crucial metabolic processes associated with photosynthesis, hormones, antioxidants or nutrient uptake (Radhakrishnan et al., 2018). Other substances that inhibit plant growth, including tenuazonic acid, isotenuazonic 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 the germination and development of weeds (Motlagh, 2012). Fungal phytotoxins are natural secondary metabolites that induce disease symptoms on agricultural, forest and weed plants. They are included into compounds such as: aromatics, aminoacids, coumarins, isocoumarins, cytochalasans, ethanones, furopyrans, nonenolides, oxazatricycloalkalenones, pyrones, spirophytotoxins, terpenes, trichothecenes, and some others with a complex and original carbon skeleton (Cimmino et al., 2015). Fungi that produce pectinase can penetrate the cell walls of weed plants by disrupting polysaccharide layers, expanding pores and releasing many lethal molecules into infected cells (Boyette et al., 2010). The extracellular lipases of fungi utilise lipids stored in the endosperm of plant seeds for growth (Thomas, 1999). Mycoherbicides can inhibit the photosynthesis of target plants. The genera *Alternaria, Chondrostereum, Colletorichum, Curvularia, Dactylaria, Diaporthe, Drechslera, Fusarium, Gloeocercospora, Microsphaeropsis, Mycoleptodiscus, Myrothecium, Phoma, Phomopsis, Plectosporium, Pseudolagarobasidium, Pseudomonas, Puccinia, Pyricularia, Pythium, Sclerotinia, Serratia, Stagonospora, Trichoderma,* and *Verticillium* have been recorded as bioherbicidal agents that inhibit the seed germination and growth of weed plants. Figure 2 shows the schematic presentation of some fungi with herbicidal activities, their toxins and mode of action on weed plants.

Tentoxin is also a fungal phytotoxin that was isolated from several *Alternaria s*pecies. Tentoxin applied on a maize farm against Johnson grass and on a soya bean farm against broad- and narrow-leaved weeds provided significant weed control (Duke and Lyndon, 2017).

Cornexistin is a fungal metabolite that has herbicidal activity. It was isolated from *Paecilomyces variotii* SANK 21086. It was successful as a post-emergence herbicide against a broad spectrum of annual weeds (e.g. cockspur, crabgrass, black nightshade, clotbur, ragweed, morning glory…), broad-leaved weeds (e.g. rough cocklebur, lamb's quarters, buttonweed, common knotgrass …) and grassy weeds (e.g. cockspur, green foxtail, crop grass…) (Fields et al., 1996).

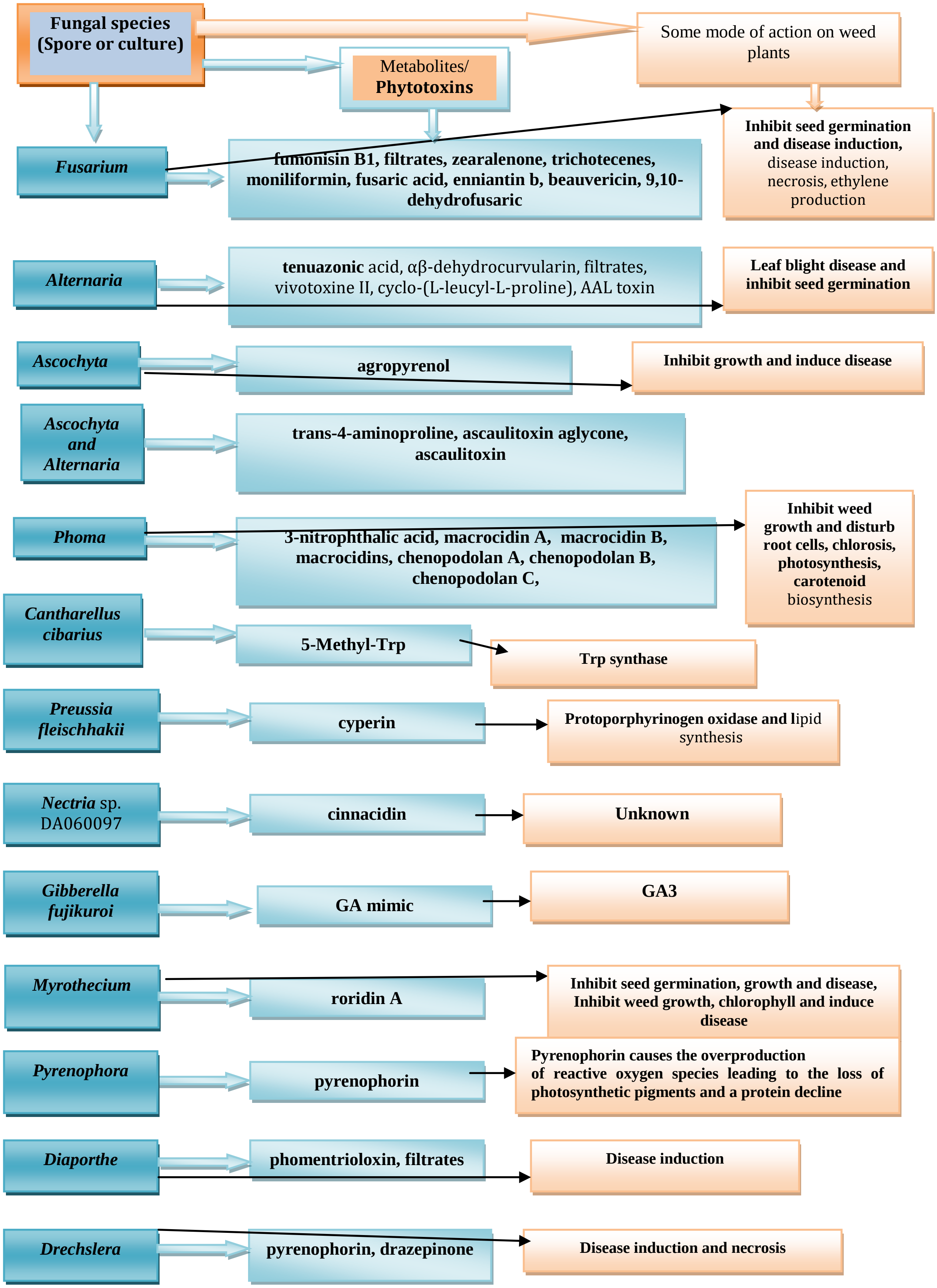

Figure 2. Genus specificity of fungal metabolites and their mode of action

Ascaulitoxin, a new uncommon phytotoxic *bis*-amino acid *N*-glucoside with herbicidal activity, was isolated from culture filtrates of the fungus *Ascochyta caulina*. This fungus causes leaf and stem necrosis of lamb's quarters and shows potential as a mycoherbicide against this harmful weed (Evidente et al., 2000).

Trans-4-aminoproline is a phytotoxic metabolite with herbicidal activity that was isolated from the fungus *A. caulina*. This metabolite shows phytotoxic activity against lamb's quarters (Vurro et al., 2001). The paper of Evidente et al. (2000) was the first report on trans-4-aminoproline as a naturally occurring compound and phytotoxic metabolite produced by *A. caulina*.

The fungal metabolite **pyrenophorin** was initially isolated from *Dreschlera avenae* and later from *Pyrenophora avenae* and *Stemphylum radicinum*. Pyrenophorin causes the overproduction of reactive oxygen species. The phytotoxicity of this metabolite is expressed as a rapid loss of photosynthetic pigments and a decline in total protein in wild oat (Aliferis and Chrysayi-Tokousbalides, 2006).

Ascosonchine, a new phytotoxic enol tautomer of 4-pyridylpyruvic acid, was isolated from the culture filtrate of the fungal species *Ascochyta sonchi*. It was proposed as a promising biological control agent for perennial sow thistle, a very troublesome weed in important agrarian crops. Ascosonchine, characterised as (Z)-2-hydroxy-3-(4-pyridyl)-2-propenoic acid, showed selective herbicidal properties, not associated with antibacterial, antifungal or zootoxic activities (Evidente et al., 2004).

Macrocidin A, a phytotoxic secondary metabolite with herbicidal activity, produced by *Phoma macrostoma*, was designed to control broadleaf weeds such as Canadian thistle and dandelion. Macrocidin A inhibits, to a degree, the biosynthesis of carotenoid enzyme phytoene desaturase (PDS). It affects chlorophyll fluorescence parameters, thus inducing photobleaching symptoms and delayed growth (Hubbard et al., 2016). Furthermore, macrocidin lowered the total chlorophyll content and reduced photosynthetic gas exchange in susceptible plants (Hubbard et al., 2015).

Studies on **chenopodolin**, a phytotoxic metaboilte isolated from the liquid culture of *Phoma chenopodicola*, have shown that it could cause massive necrotic lesions on lamb's quarter (*Chenopodium album*), creeping thistle (*Cirsium arvense*), green foxtail (*Setaria viridis*) and annual mercury (*Mercurialis annua*) (Cimmino et al., 2013b).

Curvularia intermedia, an anamorph of the fungus *Cochilobolus intermedius*, isolated from crabgrass (*Digitaria* sp.), produces the phytotoxin **α,β-dehydrocurvularin** and inhibits mitosis in root tip cells and seedling development (Jiang et al., 2008).

Moniliformin (3-hydroxycyclobut-3-ene-1,2-dione), a mycotoxin, is produced by many *Fusarium* species, particularly *Fusarium moniliforme* Sheldon. It is a water-soluble metabolite, harmful for humans and cattle. Moniliformin, as well as fumonisin and other mycotoxins produced by *Fusarium* sp., inhibits ceramide synthase. This enzyme is engaged in the synthesis of sphingolipids, which are necessary for the function of the plasma membrane and intercellular signalling. A patent has been registered for a herbicidal agent and a plant growth regulator that contains moniliformin active ingredients (e.g. cyclobuten-3,4 dione, 1-hydroxy-cyclobutendione-3,4, squaric acid…). These active ingredients control foxtail millet, perennial ryegrass, white mustard and chickweed more than moniliformin alone (Cutler et al., 2004).

Conclusions

The development of biological control, as well as sustainable agriculture in general, depends on knowledge and the awareness of the need to preserve natural resources and the environment, but also on economic factors, markets and incentives for the development of sustainable farming and environmental protection. Plant pathogens are very promising biological control agents for weeds. Not only is a long period required to study, develop, introduce and commercialise biological control agents, but integrated research, such as pathology, ecology, genetics, physiology, large-scale production, formulation and application methods, is also necessary. The study, development and final commercialisation of fungi as biological control agents face numerous obstacles, starting from basic biological knowledge to socio-economic factors. Some of the disadvantages for BCA development over chemical agents in plant disease control are the possibility of mutations, a lower level of control, no long-term control, variability, no application on large areas. The use of biopesticides requires knowledge of harmful organisms and their life cycle. Considering that their effectiveness depends on the stage of pest development, their effect is weaker than the effect of the standard chemical products. A major difficulty is also the complexity of the production of long-acting and broad-spectrum inocula. There is insufficient commercial interest, that is, markets for biological agents for weed control are insignificant, and hence, there is no interest in industrial production. Many financial institutions are reluctant to provide funds, because biological control appears to be too slow, time-consuming and unprofitable. Although biopesticides account for about 2% of the total global pesticide market, their use is growing much faster than that of chemical preparations. The existing over-dependence on chemical herbicides and weed-management decisions exclusively driven by economic interests, without taking benefits to the environment and society into consideration, are among crucial drawbacks that can hinder biological control. There are many fungi-based biological herbicides on the market of North America, one in both China and South Africa, and no such herbicides on the European market. Living fungi are active ingredients of these bioherbicides, but no fungal molecule-based product is available on the market. Reasons for this are many obstacles in the production, formulation process, environmental friendliness, and duration of herbicidal effects, and, particularly, the costs of these products (they are very expensive and need time to be registered). Bioherbicides are not available to a large degree yet, since chemical herbicides have been prevalent on the American and European markets for the last half century.

Declaration of competing interests

The authors declare that they had no conflict of interests.

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