

Chapter 11

Sorghum Allelopathy for Sustainable Weed Management



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11.1 Introduction

Weeds constitute a crucial problem in agricultural fields. Their negative impact is a result of competition with crops for nutrients (they are at the same trophic level as the crops), vie for light, water and surface area. According to Oerke and Dehne [1], crop losses resulting from weed infestation amount to 32%, while insect pests and crop diseases contribute to 18% and 15% reduction in crop yield, respectively.

The introduction in the 1940s of synthetic herbicides heavily increased the efficacy of crop protection as well as labor productivity. This method has developed rapidly, becoming a standard method contributing to decrease the significance of other weed control methods, such as agronomic, mechanical or biological.

Today, the use of weed control chemicals is being reevaluated because of their potential negative impact on food safety, human health and the environment [2, 3]. Moreover, herbicides used in simplified crop rotation contribute to the selection of weed resistance and reduces their efficacy (Fig. 11.1). In many crops and regions of the world, herbicide-resistant weeds are becoming increasingly common and consist a major challenge to science and modern agriculture.

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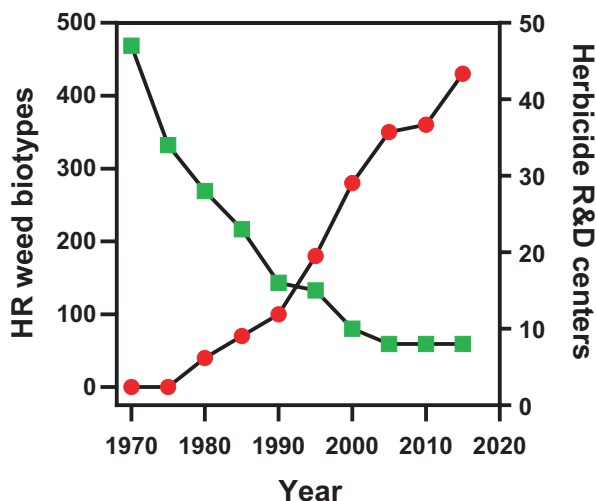


Fig. 11.1 Trends of herbicide research and development (R&D) centers (■) and herbicide-resistant (HR) weed biotypes (●) [4, 5]

Duke [6] reports that in the 1950–1970s, during the initial period of application of herbicides, new active substances (*Mechanism of action* – MOA) were commercialized every 2.5–3 years and currently 18 MOAs are used in the production of herbicides (Table 11.1). A flurry of activity has recently emerged with several new MOA being reported [7].

In the mid-1990s, the first genetically-modified crops resistant to glyphosate were introduced to agriculture production. The mechanism of glyphosate resistance has been transferred to cultivated species and transgenic crops now occupy 189.8 million hectares worldwide [8]. Many farmers use only glyphosate to manage weeds and are not actively using any other herbicides. The popularity of transgenic species is mainly due to the reduction of weed control costs and the effectiveness of weed control. The widespread use of this herbicide has contributed to the selection of glyphosate-resistant weed species and currently 45 weed species have evolved resistance to this active ingredient: *Amaranthus hybridus* L. (syn: *quitensis*), *Amaranthus palmeri* S. Watson, *Amaranthus spinosus* L., *Amaranthus tuberculatus* (Moq.) J.D. Sauer (= *A. rudis*), *Ambrosia artemisiifolia* L., *Ambrosia trifida* L., *Bidens pilosa* L., *Bidens subalternans* D.C., *Brachiaria eruciformis* (Sm.) Griseb, *Brassica rapa* L. (= *B. campestris*), *Bromus catharticus* Vahl., *Bromus diandrus* Roth., *Bromus rubens* L., *Chloris elata* Desv., *Chloris radiata* L., *Chloris truncate* R.Br., *Chloris virgate* Sw., *Cyniza bonariensis* L., *Cyniza canadensis* L., *Cyniza sumatrensis* (Retz.) E. Walker, *Cynodon hirsutus* (L.) Pers., *Digitaria insularis* (L.) Fedde, *Echinochloa colona* (L.) Link, *Eleusine indica* (L.) Gaertn., *Hedyotis verticillate* (L.) Lam., *Helianthus annuus* L., *Hordeum murinum* L. ssp. *glauicum* (Steud.) Tzvelev., *Kochia scoparia* (L.) Schrad., *Lactuca saligna* L., *Lactuca serriola* L., *Leptochloa virgata* (L.) P. Beauv., *Lolium perenne* L., *Lolium perenne* ssp.

Table 11.1 Mechanism of action of currently used herbicides [7]

Group of herbicides	Mechanism of action
Amino acid metabolism	Glutamine synthetase
	Acetolactate synthase
	EPSPS
Synthetic auxins receptors	Auxin receptor F-box proteins
	ABCB auxin transport proteins
Carotenoid synthesis	Deoxyxylulose-5-phosphate synthase
	Phytoene desaturase
	<i>p</i> -hydroxyphenylpyruvate dioxygenase
	Solanyl diphosphate synthase
Cellulose synthesis	Cellulose synthase
Folate synthesis	7,8-dihydropteroate synthase
Lipid synthesis	Acetyl-CoA carboxylase
	Fatty acid thioesterases
	Very long-chain fatty acid elongases
Mitosis	Tubulin
Photosynthesis	Electron diverters from PSI
	Blocking electron at D-1 of PSI
Porphyrin synthesis	Protoporphyrinogen oxidase
Protein phosphatase	Serine/threonine protein phosphatases
Uncoupler	Membrane disruptors

multiflorum (Lam.) Parn., *Lolium rigidum* Gaud., *Parthenium hysterophorus* L., *Paspalum paniculatum* L., *Plantago lanceolate* L., *Poa annua* L., *Raphanus raphanistrum* L., *Salsola tragus* L., *Sonchus oleraceus* L., *Sorghum halepense* (L.) Pers., *Tridax procumbens* L., *Urochloa panicoides* P. Beauv., at 30 countries and 311 locations [9].

This forced manufacturers of plant protection products to increase their spending on the search for new active substances. Gerwick [10] reported that between 1980 and 2009, 137 biologically active herbicides were launched in the market. In perspective, protection against weed infestation cannot involve new herbicides based on previously introduced mechanisms of action or on new transgenic plants resistant to marketed herbicides. The search for new MOAs is also very costly, quit often only for short-term and sometimes doomed to failure [5].

Many authors [11–13] revealed a better understanding of weed ecology in order to make greater use of integrated weed control methods. This should be based on a strong link between biology basic research and weed biology. Understanding the biology and ecology of weeds and the interaction between plants should be an integral part of sustainable methods to reduce weed infestation.

A promising phenomenon is the development of weed control based on natural products that are produced as by-products of microorganisms or plants. Only a small part of the microbiological and plant diversity has been tested for weed control. In the 1980s and 1990s, many innovative biotechnology companies discovered

and investigated active compounds that were potentially of great importance as bioherbicides, bioinsecticides or biofungicides. Obtaining glyphosate-resistant crop species in rapid development of biotechnological processes resulted in the abandonment of work on the search for biopesticides. Currently, the development of molecular techniques, genomics and metabolomics allows for more targeted and conscious research to commercialize the discovered mechanisms of activity of compounds of biological origin.

The basis for future plant protection is the understanding of physical, microbiological, hormonal and chemical inter-species and intra-species interactions. Understanding and defining the plant-plant, microorganism-plant interaction will be the foundation for the development of plant protection and its scientific basis in the future. The development of a weed control strategy will be incomplete without taking into account all available methods, in particular biological control of weeds especially implementing bioherbicides.

It is particularly difficult to develop effective and economic methods to reduce weed infestation on organic farms and weed control on such farms must be complementary used preventing, agricultural (both biological and technical) and biological methods [14]. Many different components are competitive or allelopathic in character, but also targeted in terms of activities resulting from technological development and understanding of phenomena occurring in the agricultural environment (Fig. 11.2) [15].

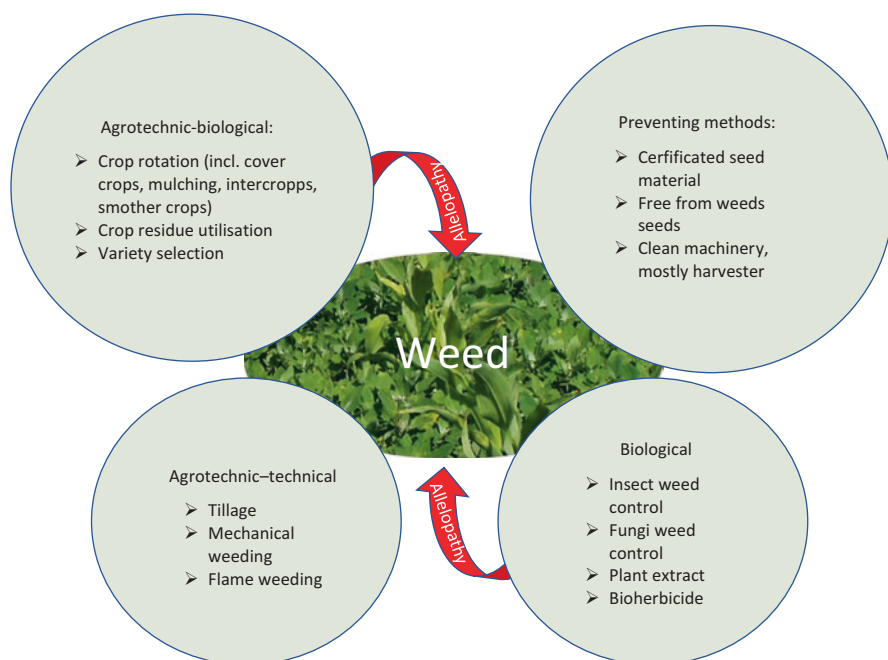


Fig. 11.2 Weed management methods. (Adapted from Kalinova) [15]

11.2 Application of Allelopathy as a One of the Methods for Biological Weed Control: Perspective and Challenges

Crop rotation and management were used for 1000 years for reduce weed abundance and biodiversity [16]. Until the 1940s, weed infestation has been managed using crop rotation systems and interventional mechanical weed control [17]. In the last several decades, chemical weed management practices have had some impact on the environment. Using knowledge of organisms for natural weed control methods are recommended [18]. Theoretically, only competitive interaction between plant species will provide the plant community with a proper structure and diversity [19]. Unfortunately, high-productivity communities – such as agricultural crops biocenosis – are characterized by less diversity due to the targeted competitiveness and reduced growth of species with less capacity to use available environment resources [19].

The plant-plant interactions are very sophisticated and difficult to distinguish character and occur at various levels. These complex interactions are based on two general relationships: competition and allelopathy (Fig. 11.3). On the basis of many studies, the interactions between plants can be successfully used in agricultural systems where the use of industrial inputs (fertilizers and pesticides) is sought. These days, there is a great need to search eco-friendly methods of weed control in modern low-input sustainable crop production systems [20]. Various studies have reported



Fig. 11.3 Competition and allelopathy differences on the mechanism as well as nature of that processes. Graph based on Qasem and Foy publication [26]

that allelopathic potential of some plants could be considered as promising alternative technique of weed management to herbicide application [17, 20, 21].

Many crops, such as alfalfa, buckwheat, corn, rice, rye, sunflower, wheat, but also sorghum have a strong impact through root exudate and realizing allelochemicals during the decomposition of biomass on weed and crop germination. Therefore, it is necessary to know the biochemical and physiological processes, but also to understand the morphological features of plants that affect the external or internal species interaction, allowing their use in limiting the growth and development of weeds.

Irrespective of the many studies confirming the stimulatory or inhibitory effect of allelopathy the advisability of its practical application in field conditions is still being questioned [22]. Detailed information has been included in review article of Głąb et al. [23]. Sometimes scientists and authors of review articles claim that “full proof of allelopathy may never be attained” [24]. Allelopathy directly and indirectly affects not only, the nutrient circulation and plant growth, but also the growth of mycorrhizal microorganism, intra-species competition and diversity as well as attractiveness for insects and other herbivorous species consist complementary natural mechanism of weed reduction [25].

González and Reigosa [22], based on studies carried out on a slope (slope direction: up – left, down – right part of graph), showed different ways of plant interaction with another plant when active compounds are exudate into soil (Fig. 11.4).

Reinhardt et al. [27], however, distinguished the following strategies for reducing weeds using the phenomenon of allelopathy:

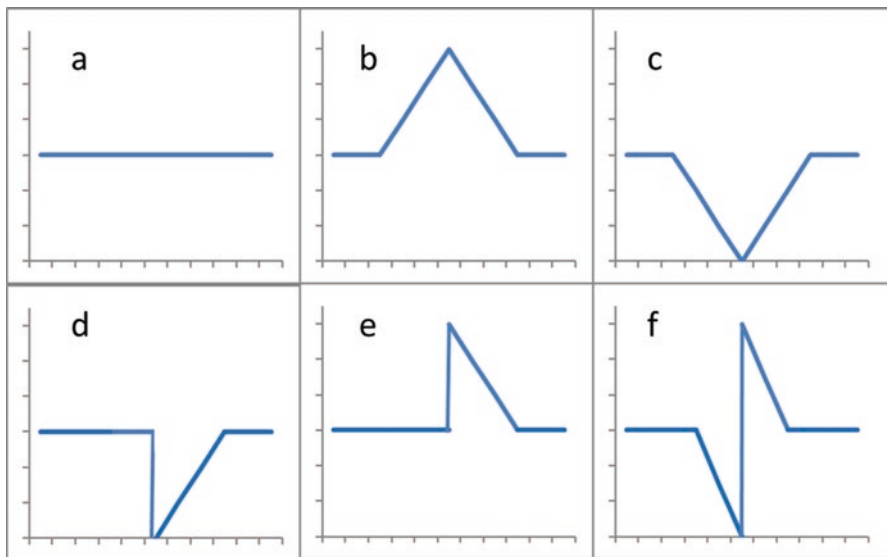


Fig. 11.4 Differences of allelochemical interaction on slope: (a) neutral, (b) stimulation, (c) competition, (d) inhibitory allelopathy, (e) stimulatory allelopathy, (f) inhibitory and stimulatory allelopathy. Based on article of González and Reigosa [22]

- use of weed smother species and breeding of these species in order to preserve such traits,
- the introduction of species with allelopathic properties for crop rotation and/or the use of post-harvest residue for mulching the field,
- isolation of allelochemicals from higher plants or microorganisms and their use as bioherbicides.

11.3 Allelopathic Effect of Living Sorghum and It’s Residues on Weeds Cultivation and Succeeding Crops

11.3.1 Sorghum in Crop Rotation

The evaluate of the allelopathic effect of sorghum on cultivated species in crop rotation, under controlled laboratory conditions and in field experiments. This effect results from the accumulation of allelochemicals in the sorghum and their slow release during biomass degradation in the soil. The subsequent effects of compounds found in various parts of the sorghum plant and the sorghum hybrid with Sudangrass have been well documented and have been the subject of much research in the last 40 years (Fig. 11.5 – adapted from Weston et al. [28]). The phytotoxicity of sorghum and sorghum hybrid with Sudangrass ranged from several to over 90% and depended on the species that was tested and also part of the plant whose

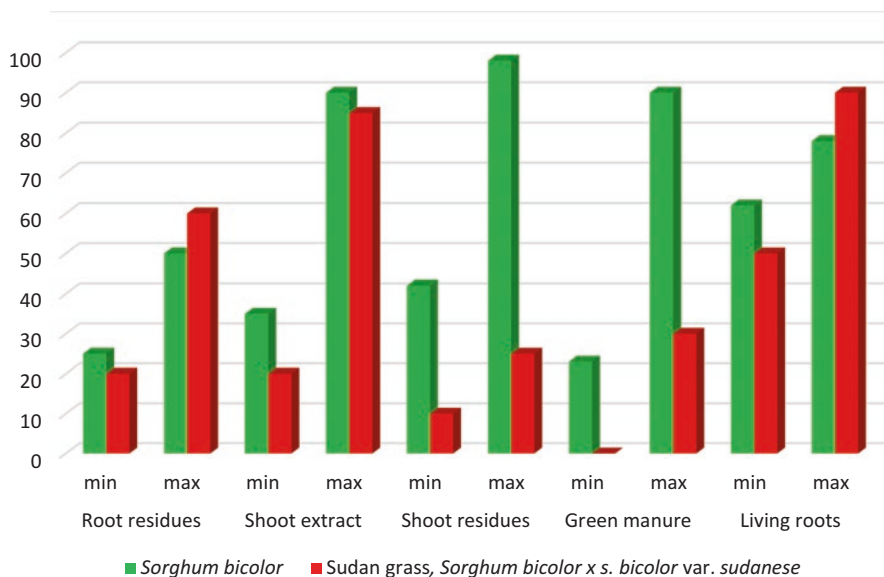


Fig. 11.5 Sorghum plants part phytotoxicity in % (base on many articles published from 1983 to 2012 years). (Adapted from Weston et al. [28])

allelopathic effect was assessed. The effect of compounds found in sorghum and sorghum hybrid with Sudangrass also depended on the weed species to which the toxic effect was directed, the development phase of the crop and weed as well as environmental factors.

Extensive global research has evaluated the after-effects of sorghum and other crops from this genera in the following areas [28]:

- use of sorghum in crop rotation and impact on other crop species,
- using an extract from various sorghum plant parts,
- use of post-harvest sorghum residues and as a cover and mulch species,
- use of sorghum as a smother species,
- use of sorghum as a component of intercropping and crop mixtures,
- utilization of allelopathic properties of sorghum with the combined use of herbicides in a reduced dose.

During the decomposition of sorghum biomass, large amounts of organic compounds are released into the environment, which may have a negative effect on the following plants, e.g. cotton germination [29, 30]. Under controlled conditions, a significant reduction in the growth of Canadian Judas (*Cercis canadensis* L.) has been demonstrated, regardless of whether fresh or dry sorghum mass is mixed with the soil [28]. The inhibition of successive plant growth was proportional to the amount of biomass introduced. This negative effect was, however, the greater where greater was the share of roots residues than stems. The effect of dried residues was also lower than fresh sorghum biomass. In the studies conducted under controlled conditions by Weston and Czarnota [31], there was an adverse follow-up effect on lettuce seedlings when the seeds were sown in rows in which sorghum had previously been grown. The authors observed that the allelopathic effect was stronger when cultivating species with small seeds. It manifested itself as dwarfism, chlorosis and, as a consequence, death of seedlings. Petersen et al. [32] reported that small-seeded species are more susceptible to phytotoxic action of residues containing allelochemicals.

In other studies, sorghum cultivation and its subsequent effects had a beneficial impact on the growth, development and yield of *Fabaceae* and *Liliaceae* family plants [33]. The root system of both sorghum and Sudangrass, secreted biologically active compounds that subsequently, positively influenced the growth of Alexandria clover, field beans, onions and contributed to a higher yield of these species. The same studies did not show a beneficial effect of sorghum and Sudangrass on plants belonging to the *Poaceae* and *Chenopodiaceae* families [33]. The assessment of allelopathic action of sorghum biomass on weeds is presented in the study conducted by Chauhan et al. [34]. Increasing the amount of post-harvest sorghum residues limited germination of *Chloris truncate* R.Br. and with 8 tons of sorghum biomass per ha, the seeds of this weed did not germinate at all (Fig. 11.6).

Post-harvest sorghum residues and associated compounds released from the residues limit the growth of many weed species in various regions of the world, e.g. *Phalaris minor* Retz., *Chenopodium album* L., *Rumex dentatus* L., *Lolium rigidum* Gaud., *Lolium temulentum* L., *Malva parviflora* L., *Carthamus oxycantha* M. Bieb.,

Fig. 11.6 Effect of sorghum residue biomass on *Chloris truncate* R.Br. emergence [34]

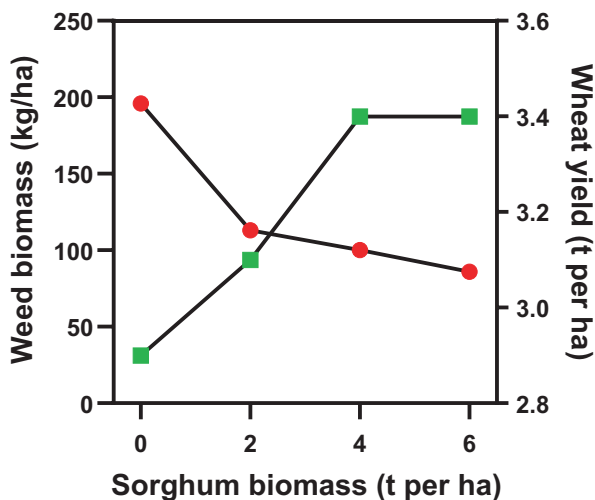
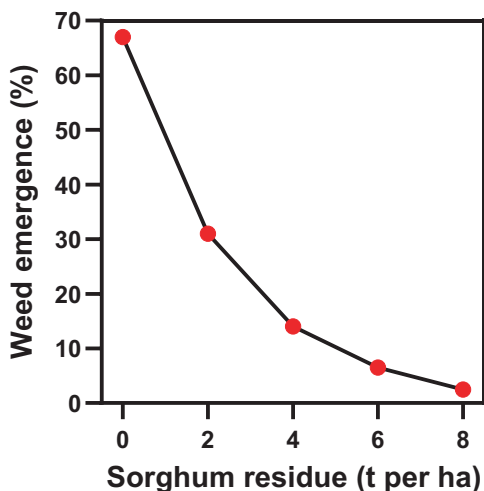


Fig. 11.7 Effect of sorghum biomass on wheat yield ■ and weed biomass ●. (Adapted from Cheema and Khaliq [39])

Silybum marianum (L.) Gaertner., *Melilotus indica* L., *Beta vulgaris* L., *Polypogon monspeliensis* L. (Desf.), *Trifolium repens* L. and *Plantago ovata* Forssk. and *Convolvulus arvensis* L. [35–37]. Sorghum biomass caused a reduction of weed mass in wheat cultivation and had a positive effect on the yield of this species (Fig. 11.7) [35]. The toxic effect of plowed sorghum biomass was observed already 1 week after the beginning of sorghum biomass degradation and it continued up to 8–10 weeks (depending on the amount of biomass absorbed) [38]. The effect on the length of *Chenopodium album* L. seedlings depended on the amount of biomass to

be broken down in the first 6 weeks after plowing, and also resulted from varietal differences and phytotoxicity of the plowed biomass.

Sorghum allelopathic potential results from different content in grains, husks, leaves, stems and roots of phenols and in particular: ferulic, *p*-coumaric, *p*-hydroxybenzoic, vanillic and syringic acids and their slow release during the decomposition of post-harvest sorghum residues. The allelopathic potential depends more on the quality of phenolic compounds than their amounts. Mallik et al. [40] reported that among gallic, syringic, chlorogenic, vanillic, caffeic, ferulic, and coumaric acids, only chlorogenic acid manifested allelopathic action on *Chenopodium album* L. In addition, the extraction of individual compounds is expensive and cumbersome from the technological point of view; and what is more frequently used instead of a mixture of compounds or water extract.

11.3.2 Crop Mixtures and Intercropping

Intercropping and crop mixtures are used in some parts of the world, mainly on small farms in tropical and subtropical zones. Environmental, production and economic effects are the main determinants of this method of plant cultivation by farmers. The scientific justification for the advisability of intercropping also emphasizes protection against erosion, limiting the rate of reduction of soil organic matter, the content and availability of nutrients, increasing soil microbiological activities and limiting weed infestation with troublesome weed species, e.g. *Striga hermonthica* (Del.) Benth [41].

In crop mixtures and intercropping, the productive effect, apart from the fundamental constituents of the environment, is also influenced by the interaction between species and access to the limiting factor of the habitat. The decision on crop mixing or intercropping depends on the degree and possibility of reducing weed infestation and infection by diseases and pests. The production technology used on a farm is another condition that should be taken into account. Therefore, the selection of plant species in intercropping should be complementary so that the cultivated species use basic environmental factors in different ways. It is necessary to analyze their suitability for such cultivation and choose agricultural technology adapted to the requirements of plants.

In the available literature, for the most part, the research results confirm that intercropping and crop mixing are more effective in reducing weed infestation than homogeneous crops [42]. Schoofs and Entz [43] and Cheema et al. [17] recommended the inclusion of intercropping as one of the basic methods of integrated weed control. Limiting the growth and development of weeds in such a system occurs through two ways, i.e. interspecies competition and the secretion of allelochemicals into the rhizosphere through the root system and their allelopathic (inhibiting or stimulating) development of the cultivated species [44]. Allelopathic interaction provides a larger balance area than just competition for an element of the environment (Fig. 11.8).

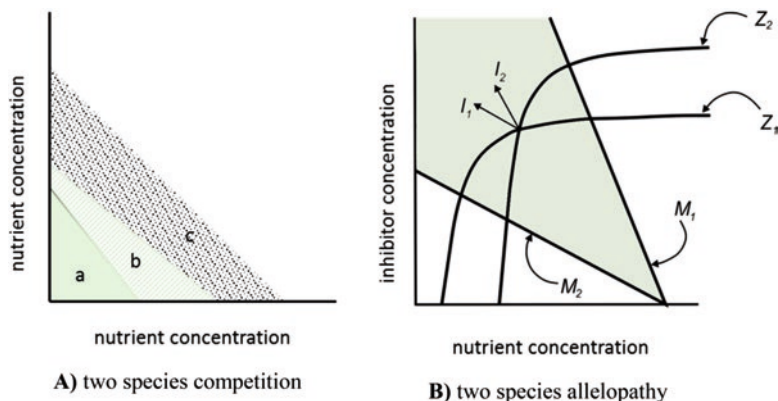


Fig. 11.8 Competition and allelopathy. Differences on Lotka-Volter model [47]. (A) Competition between two species: a – area for development of both species, b – area for development only for one species, c – area not favorable for both species. (B) Effect of allelopathy between two species compete for nutrient as an element of environment. The marked area for populations 1 and 2 (indicated by M_i) subjected stable coexistence (indicated by vectors I_i). (Adapted from Grover [48])

Growing sorghum with other crop species (mainly *Fabaceae*) is common in India, Pakistan, many African countries, as well as North and South America [28]. Many publications have confirmed that the use of sorghum as a component of such cultivation has contributed to the effective method for weeds control. Cultivation of sorghum with cotton reduced the number of *Cyperus rotundus* (L.) plants by 70–96% and the dry weight of this weed by 71–97% [44]. Similarly, intercropping of sorghum and maize significantly reduced the number of the weed species *Cyperus rotundus* (L.) by 52%, *Convolvulus arvensis* (L.) by 73% and *Trianthema portulacastrum* (L.) by 69% [45, 46]. Cultivation of sorghum with peanut and soybean proved to be very effective in limiting the number of *Striga hermonthica* (Delile) Benth., with 12% to 70% and 3% to 54% reduction in parasitic plants when sorghum was grown with peanut and soybean, respectively, compared to sorghum monoculture.

11.3.3 Sorghum as a Cover, Smother and Catch Crop

Limiting weed infestation in crop rotation without the use of herbicides is possible by sowing cover crops, smother (shading) plants, living mulch, catch crops, intercrops and protective crops [49–52]. Both smother, ground cover and catch crops are sown as a crop rotation element or after harvesting the main crop, when the remaining vegetation period allows their cultivation. The goal is not to obtain a crop that will be used for different exploitation purposes. In such cultivation methods, the produced biomass performs mainly protective functions and limits: erosion, nutrient losses and weed growth. Species sown as smother or cover plants cover the soil

and limit the access of light to weeds and inhibit their growth and competition. Limiting the growth of weeds through the cultivation of ground cover plants is supported by the secretion by the root system of chemicals that inhibit weed seed germination.

Cultivation of ground cover plants not only reduces the occurrence of annual weed species. Species used as ground cover can be used as covers to restore the naturally occurring perennial sward (plants species composition) to restore the original character of plant communities [25]. The most important species with such properties include: buckwheat (*Fagopyrum esculentum* Moench.), foxtail millet (*Setaria italica* (L.) P. Beauv.), rye (*Secale cereale* L.), sorghum spp., alfalfa (*Medicago sativa* L.), sunflower (*Helianthus annuus* L.) and some cruciferous plants [53]. Sorghum and sorghum hybrids with Sudangrass can be sown after early crops or in regions where the cultivation of other species is risky due to limited water resources [54]. The size of the aboveground mass and the ability to cover the surface make sorghum attractive as a smother and cover species (Figs. 11.9 and 11.10). During the 50–60 day vegetation period, sorghum in plastic tunnels obtained from 11.6 to 14.5 t of dry matter from ha, similar to that obtained in field conditions at 120–140 days of vegetation, and the amount of water used was up to 5 times lower than in field cultivation [54].

High value of sorghum as a smother species was reported in studies conducted by Milchunas et al. [25]. The goal of research conducted in Colorado was to restore prairie vegetation on arable land. Sorghum and wheat were sown as smother plants, and after their harvesting a mixture of prairie meadow species was sown in the following proportions:



Fig. 11.9 Sorghum as cover crops. (A) stand of 30 days after sowing (DAS), on high densities – 60 plants per square meter (3 times higher than standard). (B) Sorgho x Sudangrass hybrid at 60 DAS at first harvest cut. (Photos: J. Sowiński)



Fig. 11.10 Sorgho x Sudangrass hybrids ratoon after first cut as cover crops 3 days frost (A), 3 weeks after frost (B). Tomato cultivated on sorghum straw cover (C) (Photos: K. Adamczewska-Sowińska, J. Sowiński)

<i>Pascopyrum smithii</i> Rydb. – western wheatgrass	30%,
<i>Bouteloua gracilis</i> Willd. ex Kunth – blue grama	20%,
<i>Bouteloua curtipendula</i> Michx. Torr. – sideoats grama	20%,
<i>Nassella/Stipa viridula</i> Trin. – green needlegrass	10%,
<i>Panicum virgatum</i> L. – switchgrass	10%,
<i>Dalea purpurea</i> Vent – purple prairie clover	10%.

Sowing the mixture after wheat cultivation caused an increase in the share of annual species by 50% and exotic species by 67% compared to the botanical composition obtained when sowing was carried out after sorghum cultivation. In contrast, sowing after sorghum cultivation (as a smother species) caused an increase in coverage by native species by 245%, permanent grass species by 270% and western wheatgrass by as much as 811% compared to the coverage of surface after wheat sown as a smother plant. The high usefulness of sorghum resulted from the limited availability of nitrogen, which contributed to the increase in the share of annual species, in particular kochia (*Bassias coparia* (L.) A.J. Scott.) and Russian thistle (*Salsola tragus* L.) after using wheat as a smother species. In addition, the allelopathic effect of sorghum sown as a smother plant limited the growth of alien, invasive species and contributed to the good development of western wheatgrass [25].

Difficult conditions during the occurrence of drought as well as the type of soil can potentially affect the effectiveness of allelopathy and allelopathic activity of compounds found in individual plant species.

The phenomenon of allelopathy and the presence of rhizosphere fungi and other microorganisms mean that crops using sorghum as a ground cover contribute to improving the physical and chemical properties of the soil, and also allow the renewal of land and restore natural communities.

11.4 Effect of Sorghum Allelochemicals on Weeds

In an ecosystem, many important interactions are based on chemical regulations and a wide group of chemical compounds that directly or indirectly affect plants. These relationships occur between populations or between processes occurring within a population, taking various forms: commensalisms, competition, mutualism, and pathogenesis. These compounds interact in different ways, and relationships between species are from neutral through favorable to unfavorable (Table 11.2). The most important of them belong to the following groups: enzymes, vitamins, hormones, chelates and allelochemicals. Groups of chemical compounds that are secreted into the environment by leaching, decomposing, volatilizing or root secretions and at the same time have an impact on the biological processes that occur between plants are called allelochemicals [15]. In many species they occur in all parts of plants such as: leaves, stems, flowers, pollen, seeds and fruits, and roots.

Sorghum is a crop with high allelopathic ability and its active compounds are distributed in different parts of the plant. The range of action of allelochemicals is wide – from changes in physiological and biochemical processes, through the activation of cell division and anatomical changes in the cell. Some of them inhibit the process of photosynthesis and respiration and increase oxidative stress, contributing to the accelerated process of cell death and, consequently, the entire weed plants [55]. The assessment of the suitability of plants as an allelopathic species is often possible by determining their total content of phenolic compounds.

During the growing season as well as during the decomposition of biomass, compounds released to the environment are usually an organic mixture that can interact through synergism modified by other environmental factors. In the conditions of rainfall deficiency, high temperature, severe disease and pest infestation or nutrient deficiency, the allelopathic effect is stronger [56]. In conditions of high soil moisture, cloudy weather and intensive rainfall, the content of allelochemicals and their activity is lower [57]. High soil moisture stimulates biological activity and sorption

Table 11.2 Different interaction between plants

Interaction type	Species first	Species second
Mutualism ^a	↑	↑
Commensalism ^a	↑	=
Competition	↓	↓
Allelopathy	↑	↓
Herbivory ^a	↑	↓
Predation	↑	↓
Parasitism ^a	↑	↓
Amensalism	↓	=

^a some specific interaction is called symbiosis – Mutualism, Commensalism, Herbivory, Parasitism
Interaction unfavourable (↓), favourable (↑), neutral (=)

of allelochemicals by soil particles and as a consequence, allelochemicals become biodegraded by microorganisms.

Sorghum contains many substances that have allelic character and allelopathic effect. The basic one is sorgoleone, produced by root hair. It has a strong limiting effect on the growth of other species, including crops [58].

There are many compounds in sorghum biomass and their usefulness has been evaluated in various conditions (laboratory, controlled and field): chlorogenic, *m*-coumaric, *p*-coumaric, caffeic, *p*-hydroxybenzoic, ferulic, vanillic, syringic, gallic acids, and *p*-hydroxybenzaldehyde [36, 38, 59, 60].

In the aboveground parts of sorghum and sorghum hybrid with Sudangrass, there are hydroxybenzoic acid and *p*-hydroxybenzaldehyde, which inhibit the growth of seedlings of annual weed species [28]. However, better toxic effects were obtained under controlled conditions than in the field ones. The authors account for the differences with the rapid rate of degradation in non-sterile field conditions. Similarly, the activity of phenolic compounds was short-lived and unstable in field conditions [60].

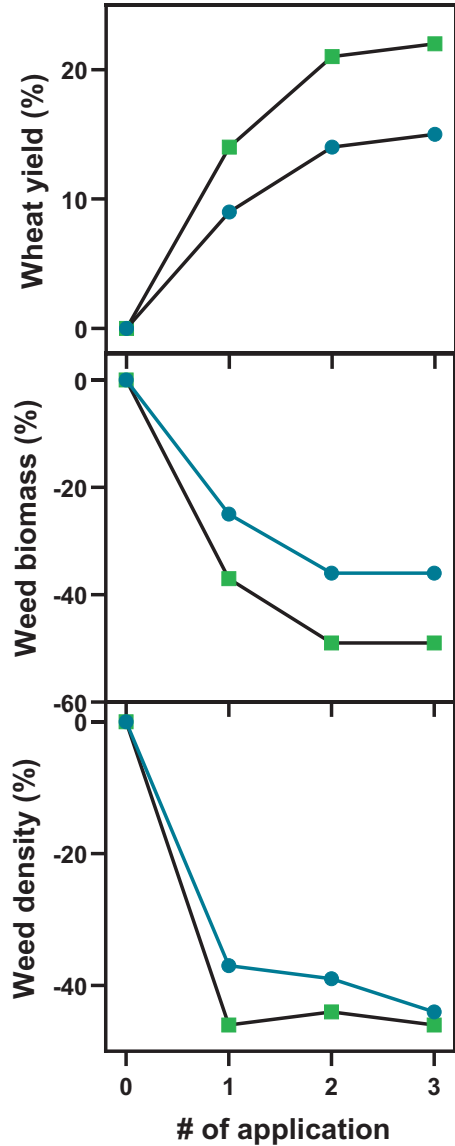
11.4.1 Allelochemicals in Aboveground Sorghum Parts as a Source of Sorgaab

Water extracts of organic acids from sorghum plants prepared according to the procedure described by Cheema and Khaliq [39] are called sorgaab. They can be made from fresh and dried parts of sorghum plants. Preparation of sorgaab is easy, cheap and does not require a specialized laboratory. The sorghum material (leaves, stems or whole plants) cut into 2 cm sections are soaked at room temperature in distilled water in 1: 20 ratio for 24 h. For easier use after preparation, the extract should be filtered and sterilization at 100 °C for 20 min is recommended. Sorgaab can be used fresh, immediately after preparation or stored frozen (−15 °C) and applied at any time depending on the needs.

Sorgaab contains various water-soluble compounds. Mahmood [61] distinguishes 14 chemicals that are water-soluble and easily go into solution. Iqbal and Cheema [62] determined the occurrence of the following phenolic compounds: gallic, protocatechuic, syringic, vanillic, *p*-hydroxybenzoic, *p*-coumaric, and benzoic acids. Parveen [63] and Nielsen et al. [64] showed the presence in sorgaab of the following: caffeic, ferulic, chlorogenic, syringic and vanillic acids, as well as dhurrin and *p*-hydroxybenzaldehyde.

The limiting effect of sorghum plant extracts on weeds and their beneficial impact on cultivated species has been confirmed in many publications. In the studies by Cheema et al. [35] the concentration of sorgaab used and the number of treatments carried out had an impact on the number and weight of weeds and increased wheat yield (Fig. 11.11).

Fig. 11.11 Effect of number of sorgaab application applied as either 5% (●) or 10% (■) concentration (w/v) on wheat grain yield, weed biomass and weed density. Sorgaab was applied either at 1 – 30 DAS (days after sowing), at 2 – 30 and 60 DAS or at 3 – 30, 60 and 90 DAS compare to control (0) without sorgaab application



In the conducted tests, the most sensitive weed species to the applied sorgaab were: *Chenopodium album* L., *Phalaris minor* Retz., *Avena fatua* L., *Convolvulus arvensis* L. *Coronopus didymus* L. (Sm.), *Fumaria parviflora* Lam. and *Rumex dentatus* L. On the other hand, however, the sorghum water extract stimulated the growth of *Melilotus parviflora* Desf. [35].

11.4.2 *Sorgoleone – The Main Sorghum Allelochemical as a Bioherbicide*

Sorghum is an allelopathic crop that represses the growth of weeds by exuding a number of lipophilic benzoquinones (referred to as sorgoleone) from its root hairs. The most abundant form is 2-hydroxy-5-methoxy-3-[(Z,Z)-8',11',14'-pentadecatriene]-*p*-benzoquinone [65] (Fig. 11.12) and its resorcinol derivative, which accounts for 90% of compounds that are present in the root exudates [66, 67]. The remaining 10% of root exudate components include sorgoleone analogues with vary in the degree of saturation of the aliphatic side chains and their respective resorcinols derivatives [68].

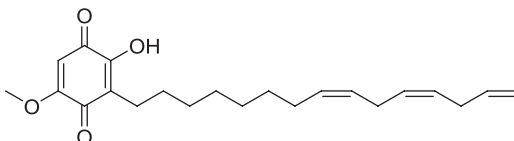
11.4.2.1 Herbicidal Activity

Sorgoleone extracts are not very potent when applied postemergence. This is due to the extreme lipophilic nature of this molecule. It does not readily absorbed nor translocated in mature leaves, although sorgoleone does penetrate into hypocotyls and cotyledons [37]. Herbicidal activity was improved via formulation of sorgoleone as a wettable powder [4.6WP]. Broadleaf species were more susceptible than grass weed species. Preemergence application of sorgoleone completely suppressed germination and growth of broadleaf weed species at 0.2 g a.i. L⁻¹ active. *Rumex japonicus* Houttuyn. and *Plantago asiatica* L. were most sensitive to sorgoleone, with 100% control following postemergence application of 0.4 kg a.i. ha⁻¹ sorgoleone. Most other broadleaf weeds were 90% controlled at that rate. On the other hand, crop species were less sensitive to sorgoleone, with no more than 30% inhibition at the highest rate of 0.4 kg a.i. ha⁻¹ [69].

Another approach has been to mix sorgoleone extracts with extracts from other plant species.

A mixture of sorgoleone and root extract of tartary buckwheat (*Fagopyrum tataricum* Gaertn.) was much more active than either extracts alone. Consistent with other studies, broadleaf weed species (e.g., *Galium spurium* L., *Rumex japonicus* Houttuyn., *Aeschynomene indica* L., and *Amaranthus retroflexus* L.) were more susceptible than grass weed species. This example of enhanced suppression of weed growth by sorgoleone and with tartary buckwheat root extract suggests interesting possibilities for effective weed management under organic farming situations [70].

Fig. 11.12 Structure of the main sorgoleone analogue



11.4.2.2 Mechanisms of Action

Detailed studies on the phytotoxic activity of sorgoleone demonstrated that its mechanism of action targets the electron transport chains. With regard to photosynthetic electron transport [71, 72], sorgoleone is structurally similar to plastoquinone (a lipid benzoquinone) (Fig. 11.13a), resulting in competition with the natural electron acceptor at the plastoquinone binding site on the D1 PSII protein (Figs. 11.13b, c and Fig. 11.14) [37, 73].

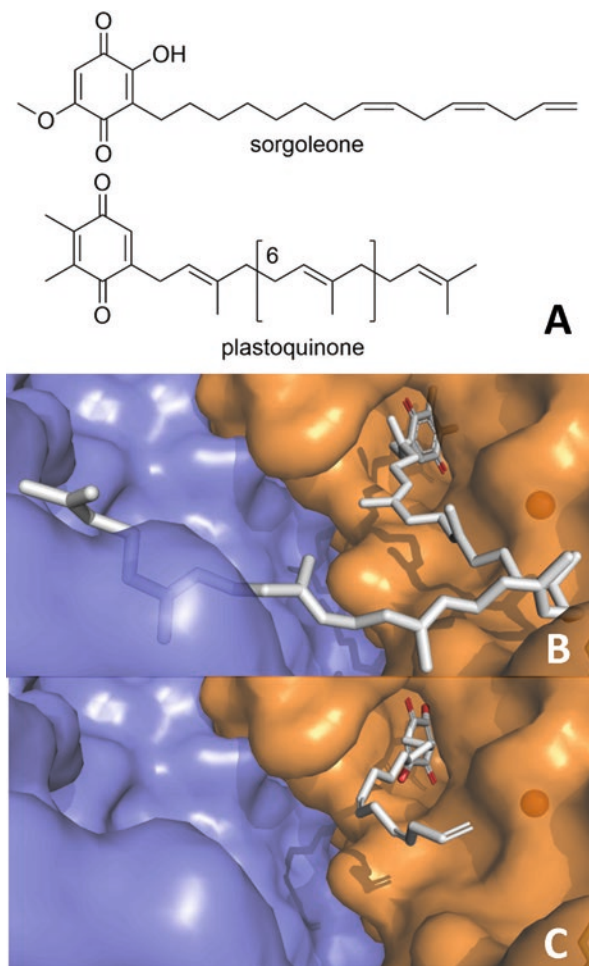
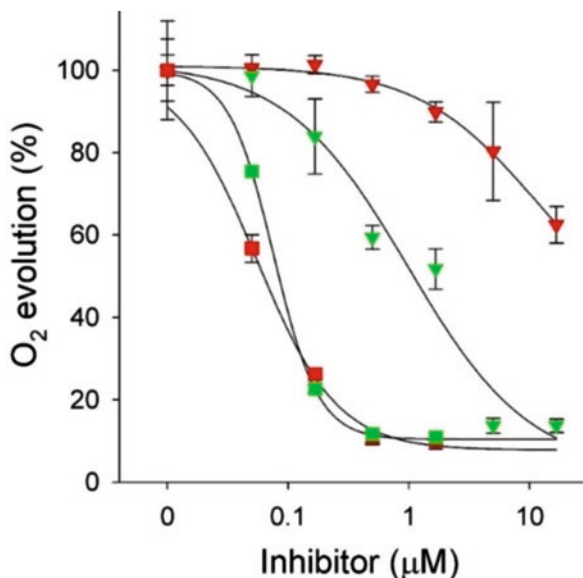


Fig. 11.13 (A) Structure of sorgoleone and plastoquinone. (B) Plastoquinone binding domain (QB) on the D1 protein (gold color) of photosystem II obtained from the crystal structure analysis of photosystem II complex (3wu2) [74], with a close view of plastoquinone binding on QB. (c) Modeling of sorgoleone binding in the plastoquinone binding site. Structure of minimized sorgoleone was obtained from Lebecque et al. [75]

Fig. 11.14 Effect of sorgoleone (square) and atrazine (triangle) on oxygen evolution from thylakoid membranes isolated from wild-type and triazine-resistant redroot pigweed (*Amaranthus retroflexus* L.). ▼ = wild type with atrazine; ▼ = resistant with atrazine; ■ = wild type with sorgoleone; ■ = resistant with sorgoleone adapted from Dayan et al. [37]



An additional mechanism of sorghum phytotoxic activity [76] is the reduction of carotenoid production through inhibition of *p*-hydroxyphenylpyruvate dioxygenase (HPPD), a key enzyme in carotenoid synthesis and the target site for triketone herbicides. Carotenoid reduction leads to a decreased amount of chlorophyll and subsequent reduced photosynthetic capability. Sorgoleone was tested along with 33 other natural products of various structural classes on HPPD. Recombinant HPPD from arabisidopsis is sensitive to several classes of natural compounds including sorgoleone. While the triketone natural products were competitive tight-binding inhibitors (showing parallel lines in the protein titration assays) (Fig. 11.15a), sorgoleone did not bind tightly to HPPD (showing conversion lines in the titration assay) (Fig. 11.15b).

Additionally, sorgoleone lowers the membrane activity of H⁺ ATPase, which, in turn, leads to disturbances in water uptake [77]. While the participation of this activity on weed control is not well understood, it is interesting that this natural product interacts with more than one target site, suggesting that evolution of resistance to sorgoleone may not be very likely.

11.5 The Area of Future Research

Based on the experience gained during the last 50 years of intensive use of herbicides, we should understand that by introducing new MOAs we will not be solve the problem of weed infestation. Herbicides, as well as mineral fertilizers and other plant protection products, have contributed to the increase in the productivity of

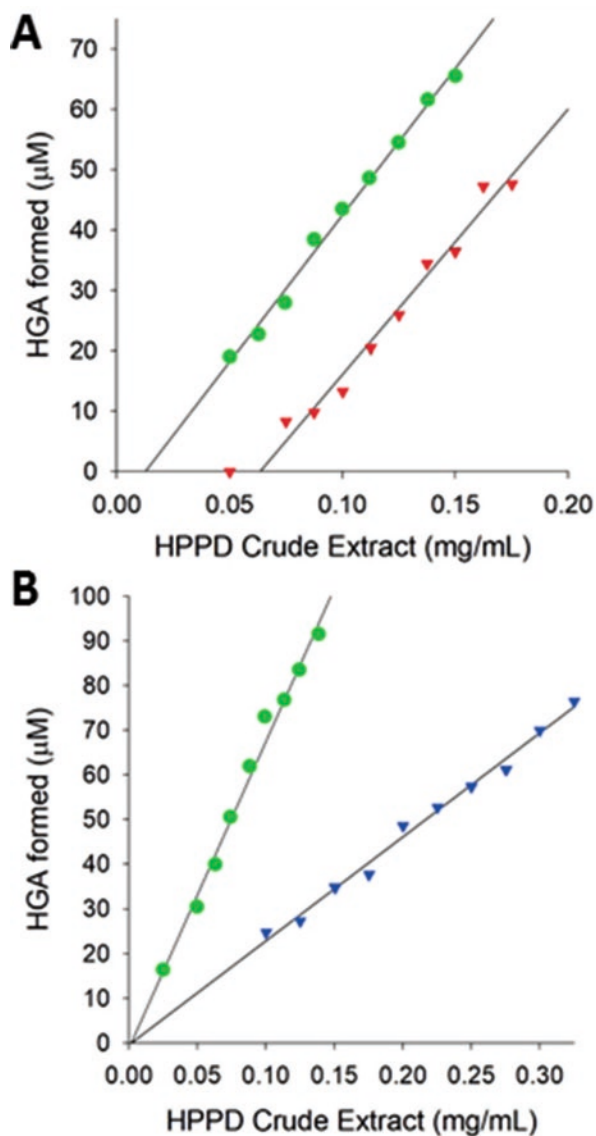


Fig. 11.15 HPPD inhibition kinetics of (A) the β -triketone usnic acid, (B) the *p*-benzoquinone sorgoleone. ●=no inhibitor; ▼ = 0.03 μ M(-)-usnic acid and ▼ (= 1 μ M sorgoleone). (Adapted from Meazza et al. [76])

arable crops, while heavily burdening the environment [78]. We should learn that herbicides are only a small part of the solutions that can be used in weed control [79]. Sustainable weed control is a key action for both organic and conventional agriculture. Reducing the occurrence of weeds requires the introduction of new comprehensive methods in addition to the already existing ones.

The use of the phenomenon of allelopathy and organic compounds produced by plants should be a future-oriented area of intensive research and implementation. Sorghum and its forms contain many significant substances that affect other plants and animals (dhurrin). Sorghum with its allelopathic properties should be used as an element of crop rotation, sown as a ground cover, mulch plant or in intercropping. The importance of sorghum in crop rotation and the use of its post-harvest residues should result not only from the increase in soil organic matter content, but also its effect on reducing weed infestation.

In the future, the main area of research and implementation should be focused on the use of compounds present in sorghum, in particular sorgoleone. This is due to the following properties of this compound:

- it is toxic to dicotyledonous and monocotyledonous weeds in very low i.e. 10 μM concentrations [80, 81].
- its postemergence application at a dose comparable to atrazine (0.6 kg a.i. ha^{-1}) inhibits the growth of most 14-day-old weed seedlings [82].
- its pre-emergence application is toxic to small-seeded weed species [31].

This is confirmed by the advanced work on sorghum gene mapping and the recognition of the *SOR1* gene, which codes fatty acid desaturase (FAD), the enzyme responsible for the synthesis of sorgoleone in sorghum roots [83].

The expression of this gene is strongly differentiated in sorghum plant parts and the relative values according to Yang et al. [83] were as follows (assuming the initial content in the stems):

Stem	1.0
Immature leaf	1.3
Panicle	1.6
Root with hair removed	4.1
Mature leaf	4.4
Root hair	4369.7

More recent work characterized the function of the fatty acid desaturases responsible for the biosynthesis of sorgoleone [84]. Research attempting to transfer the genes encoding key enzymes involved in the production of this natural herbicides to other plants is on-going.

Research is currently underway to determine the importance of plants in influencing on and modification of the nitrification process. Many studies in this area confirm the ability to reduce nitrification by the secretion of secondary metabolites into the environment by root hairs of many plant species [85, 86]. This process is called biological nitrification inhibition (BNI) and it has been well described in

species such as *Brachiaria* [87, 88]. The results of the first research conducted on cultivated plants showed that sorghum (specifically sorgoleone) manifests strong ability to modify the nitrification process [89].

Interesting results were obtained by Maqbool and Sadiq [90] after applying sorgaab in the form of spraying on maize seedlings. Phenolic compounds from sorghum increased maize resistance to drought and net photosynthesis, the efficiency of water utilization was highest when 1.0–1.5 mL of phenolic compounds per 1 litre of solution was applied.

11.6 Conclusions

One of the many common, transdisciplinary goals for scientists working in the field of agriculture should be to decrease weed infestation with limited or no negative impact on the environment. From a social and demographic points of view, it is also important to ensure food security for the world's growing population up to 9 billion in 2050 [91]. To sum up, we should be optimistic that this must be the case and that future herbicides along with their new modes of action will be discovered through the integrated use of biological methods, i.e. modern “-omics” techniques of genomics, proteomics or metabolomics in combination with traditional biology [92].

Biotechnology-based transgenic plant breeding has been developing actively since the mid-1990s. In addition to the unquestionable benefits for the global economy and food security, new threats are emerging, such as weed resistance through the transfer of the gene responsible for modification of the gene from the crop to weeds. Corrective actions should be taken now and solutions for the future should be sought. In contrast, compounds found in plants also in sorghum provide biological protection through the production and secretion of compounds that can be used to limit the growth and development of weeds.

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