



Allelopathy as a source of bioherbicides: challenges and prospects for sustainable agriculture

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Received: 13 February 2023 / Accepted: 27 April 2023 / Published online: 10 May 2023
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Abstract The sustainable management of the environment and crop production in modern agriculture involves dealing with challenges from climate change, environmental pollution, depletion of natural resources, as well as pressure to cope with dependence on agricultural inputs. Balancing crop productivity with environmental sustainability is one of the main challenges for agriculture worldwide. The emergence of weeds resistant to synthetic herbicides generates huge economic losses, so unconventional weed control strategies, especially those based on ecological principles, are very much needed in modern agriculture. Incorporating a natural eco-friendly approach—allelopathy—as a tool in an integrated weed control plan by growing specific crops or spraying fields with extracts containing allelopathic compounds can significantly reduce the use of herbicides. Allelopathy is considered a multi-dimensional phenomenon occurring constantly in natural and anthropogenic ecosystems, by which one organism produces biochemicals that influence the growth, survival,

development, and reproduction of other organisms. The objective of this systematic literature review is to present a comprehensive overview of allelopathy, define this phenomenon, and classify allelochemicals. This paper also discusses and highlights recent advances, ongoing research, and prospects on plant allelopathy management practices applied in agriculture, and the underlying allelopathic mechanisms. The review suggested the holistic view of some allelochemicals as an ecological approach to integrated weed control and is an important contribution to future research directions of multidisciplinary programs, chemoinformatic tools, and novel biotechnology methods to plant breeding.

Keywords Allelopathy · Bioherbicides · Sustainable agriculture · Secondary metabolism · Weed management · Allelochemicals

1 Introduction

One of the most important elements to sustaining life and promoting good health is ensuring access to enough safe and nutritious food. It is estimated that the agro-tech sector may encounter many difficulties in securing food production for the rapidly growing human population in the coming years. The world's population is expected to increase by 2 billion persons in the next 30 years, from 7.7 billion currently to 9.8 billion in 2050 (Hernandez-Tenorio et al. 2022). Out

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of the United Nations' 17 sustainable development goals, the second goal focuses on agriculture, aiming for zero-hunger levels worldwide while also being sustainable over time (OECD/FAO 2022). Sustainable agriculture can be defined as meeting the food needs of a growing world population while ensuring minimal impact on the environment and humans as well as productivity (Lykogianni et al. 2021). To withstand these harsh challenges induced by abiotic and biotic factors the world needs to adopt novel and improved agricultural practices and strategies for high sustainability and productivity (Khurshed et al. 2022). Among the major biotic constraints, weeds are considered the most harmful to agricultural production (Gharde et al. 2018). Worldwide huge crop losses have been found to result from heavy weed infestations. Crop losses due to weeds continue to reduce the available production of food and cash crops worldwide. It is very difficult to indicate the yield loss due to any single weed species; therefore, the loss is estimated as the collective effects by all weed species. Globally, compared to other biotic factors, weeds produced the highest potential loss at 34%, with animal pests and pathogens being less important—with losses of 18 and 16%, respectively (Głąb et al. 2017).

Integrated Weed Management is a long-term comprehensive approach to controlling and mitigating infestation in fields incorporating physical, genetic, biological, cultural, and chemical weed management techniques (Jabran et al. 2015). Farmers usually rely on quick and effective synthetic herbicides which represent the backbone of the agri-food sector in its endeavor to secure food production and suppress yield losses, but their application is perceived as an obstacle to the achievement of sustainability (Lykogianni et al. 2021). The excessive use of chemical herbicides has contributed significantly to soil degradation, environmental pollution, and adverse effects on non-target organisms and has been proven to have deleterious effects on human health. The consequences of the inappropriate adjustment of herbicides to the weed species occupying the fields, the use of herbicides at the wrong plant developmental stage and under unsuitable weather conditions are the accumulation of active compounds in the soil, the accumulation of weed species, and the acceleration of the evolution of resistant biotypes (Motmainna et al. 2021). Long-lasting exploitation of herbicides with one target site in plants has resulted in the evolution of weeds resistant

to herbicides (Soltys et al. 2013). The complete exclusion of chemical control of weeds is impossible with current agrochemical practices, so it is necessary to develop novel classes of herbicides with new mechanisms of action and target sites. Reducing the large-scale use of herbicides and introducing organic production systems requires the combined efforts of all actors in the food value chain (Möhrling and Finger 2022). In the face of climate change, increasing consumer awareness of crop protection products and fertilization, coupled with unconventional methods to ensure safe and superior agricultural products are in high demand (Głąb et al. 2017).

The need for safe food production and eco-friendly trends in weed management forces scientists to develop innovative solutions. There is a growing need for new herbicides with safer toxicological and environmental profiles. Natural compounds provide a wide selection of potential new environmentally safe herbicides, so-called “bioherbicides”, which are based on compounds produced by living organisms (Soltys et al. 2013). Bioherbicides are broadly defined as products derived either from living organisms or their secondary metabolites to suppress target weed populations without harming the environment (Scavo and Mauromicale 2021).

Recently, among the proposed approaches, research on allelopathy has become increasingly prevalent in weed management for agroecosystems (Hoang Anh et al. 2021). Allelopathy, through its wide range of benefits, may become a promising solution to the problems of environmental pollution and the evolution of herbicide resistance (Jabran et al. 2015). Allelopathy, known since ancient times, is a natural phenomenon in which different organisms affect the functioning of other organisms in their vicinity, negatively or positively by releasing secondary metabolites (Bajwa 2014). The phytotoxic properties of allelochemicals, or biologically active metabolites exuded by higher plants, fungi, or microorganisms provide a source of practical solutions for weed control.

Allelopathic compounds are a suitable substitute for synthetic herbicides because they do not have residual or toxic effects, however, so far only 3% of the approximately 400,000 known compounds in plants that show allelopathic activity have been recognized as acting as bioherbicides, although more than 2000 plant species (39 families) have strong

allelopathic effects (Li et al. 2019). The deployment of allelopathic cover crops, intercropping, the inclusion of allelopathic plants in crop rotation, and the use of their residues as mulch are important for ecological, sustainable, and integrated weed control systems (Jabran et al. 2015). The most significant challenge to sustainable modern crop protection is the limited availability of bioherbicides. For current researchers, allelopathic plants can be a source for identifying and isolating new allelopathic substances. After examining their bioactivity under laboratory and field conditions, promising compounds can be recommended for novel natural herbicide development for sustainable agriculture (Motmainna et al. 2021). Despite their many advantages, allelochemicals have some limitations for direct use as bioherbicides. It is complicated to explain the different modes of action of each class of allelochemical and to determine how environmental conditions affect their success. Problems in their commercial deployment arise from the complexity of application in crop fields due to easy degradation, and the complicated registration processes required by authorities.

This article presents a comprehensive and updated review of the herbicidal potential of allelopathy. The discussion begins with a description of the origin of allelopathy and an explanation of the controversy over the proper definition of the allelopathy phenomenon and its characterization in a mathematical model. Furthermore, the physiological and ecological mechanisms underlying plant allelopathy, factors influencing the release of allelochemicals, examples of selected secondary metabolites, and classification of allelochemicals are highlighted in this overview. Consideration is also given to the world's major plant crops that exhibit allelopathic potential and strategies such as intercropping with allelopathic weed plants, the use of allelopathic cover crops and residues, and rotational sowing of allelopathic plants for practical weed control in field crops are discussed. The paper discusses examples of new tools of molecular genetics, proteomics, and metabolomics, as well as modern and sophisticated methods of chemistry and biochemistry that could lead to the development of substances, perhaps based on the structure of particular compounds found in nature, that could be used without risk as selective and eco-friendly herbicides. The publication compares and critically evaluates the effectiveness of synthetic plant protection products

with those of natural sources. Finally, a reflection on existing problems and suggestions for future research directions in this field is presented to provide a useful reference for forthcoming studies on plant allelopathy and its use in the creation of new bioherbicides with novel, unexploited target sites.

2 Genesis and definition of the allelopathy phenomenon

A detailed literature review determining the origins of the term allelopathy leads to the work of Hans Molisch in 1937. The more historically oriented students recognized A.P. de Candolle's theory of the early nineteenth century as a starting point. Reviewing the literature, it is apparent that the history of allelopathy has only been superficially investigated, even though it has been very popular in plant ecology over the last decades. In the book "The History of Allelopathy" Willis tried to bring to light most of the writings that have touched on allelopathy spanning the period from antiquity until about 1957. In the mid-1950s there were almost synchronous publications of three books about allelopathy: a 1955 monograph by Grümmer in German, a book on the effects of allelopathic substances in agriculture by Chernobrivenko (1956) in Russian, and a little-known but valuable monograph in English by Hubert Martin (1957) entitled *Chemical Aspects of Ecology in Relation to Agriculture* (Willis 2007).

This should be emphasized that allelopathy is not a completely new phenomenon, it has been described in the literature already for more than 2000 years. The first references to the general 'sickening of the soil' by plant toxins that negatively affected the growth of other plants were published in ancient manuscripts. After reading Willis's book, which contains an extensive collection of examples of theses by classical authors from Ancient Greece and Rome, can conclude that the concept of allelopathy and the controversy surrounding it has been with us for a very long time. Although it is discussed and quantified in a relatively large number of papers, the existence of allelopathy as a natural ecological process is still considered doubtful by many.

The idea of allelopathy and its genesis has been very superficially investigated, but with the growing trend in plant ecology, it is once again in the spotlight.

Molisch derived allelopathy from the two Greek words: “*allelos*”, mutual, and “*pathos*”, suffering (Molisch 1938). Although the Greek term was translated as mutual harm, Molisch in his discussion indicated that the meaning of allelopathy should include any direct or indirect effect of one plant or microorganism on another. He emphasized that for him the phenomenon includes both harmful and stimulatory interactions on the target organism and surrounding organisms (Willis 2007). Molisch’s definition was expanded and used in the practice to describe the chemical communication and chemical interactions between different organisms in general. The chemicals involved in this process, called allelochemicals, can be primary metabolites (directly involved in fundamental physiological processes of an organism) or secondary metabolites, which are not contributing to the survival of plants but produce some products that aid them in their normal growth and development (Chaïb et al. 2021).

Based on previous definitions of allelopathy and attempts to explain its mechanism of action, the International Allelopathy Society (IAS), defined allelopathy as the science that “studies any process involving secondary metabolites produced by plants, algae, bacteria, and fungi that influence the growth and development of agricultural and biological systems” (Duke 2010). One of the most contentious points in determining the definition of allelopathy is to distinguish it from the phenomenon of competition. In the environment it is impossible to separate these two mechanisms, therefore scientists recognize allelopathy as part of the competition for resources. This arisen can be solved by Muller’s proposed term “interference” as a general influence between plants, thus encompassing both allelopathy and competition (Rice 1984). Allelopathy is different from the competition the fact that it involves the removal or reduction of some factor from the environment that is required by some other plant sharing the habitat (Chaïb et al. 2021). Competition is related to the acquisition of various resources: light, water, food, minerals, pollinators, and root space. In an environment of insufficient supply, a simple way to survive is to inhibit the growth of competitive plants and thereby decrease the consumption of limited resources by those competitors.

The allelopathic effect is largely stress-dependent. In practice, a plant for example, if it is deficient in mineral elements would suffer both the

phytotoxic effect of allelopathic compounds and the stress of nutrient deficiency, so its growth would be inhibited. This can be evidenced by the fact that competition is often associated with 43–57% of interference (An et al. 2008). This supports the idea that one effective means of plant action is the release of phytotoxic substances into a shared habitat to inhibit the growth of competing plants, which would confirm Bais’s “novel weapons hypothesis” thesis about allelopathy for invasion success (Bais et al. 2003). When considering a more complex environment than a simple laboratory-scale experiment, it is important to include all factors that may influence the allelopathic effect, which can be additive, synergistic, or antagonistic.

Allelopathy has been viewed in a multifaceted approach, as shown by a growing number of works by scientists from diverse fields worldwide. Academics also began to develop mathematical modeling to separate the concept of allelopathy from the competition, establishing the fundamentals of allelopathy and its ecological role. Only a few authors have been challenged to develop an allelopathic interaction model based on experimental data or field studies (An 2005). They proposed a model for considering allelochemical production that is based on the principles: (1) release and degradation are not reversible, (2) the amount of compounds released is proportional to the rate of degradation of the allelochemicals, (3) the amount of allelopathic compounds in plants is proportional to the rate of their release, (4) considered is the total allelochemical production, (5) the production, transformation, and decomposition of allelochemicals are considered a system, which consists of two processes, i.e. allelochemical release and dissipation, and three compartments (An et al. 2003). Such generalized model processes, while not always satisfactory, will be useful in explaining patterns of species interactions and point the way to further research. An (2005) develop the assumption that the allelochemical content in living plants declines with age and plant stress and is reflected by the corresponding dynamics in the environment. Under normal conditions, the concentration of allelopathic compounds can be relatively stable in the plant and these biomolecules can be in an inactive state. This mathematic study may enable us also to understand why the results of allelopathic research are inconsistent when conducted under different stages of plant growth, and

why results change as experimentation proceeds (An 2005).

3 Mechanism of action of allelochemicals

Over the years, the phenomenon of allelopathy has been well documented, while the precise understanding of the mechanisms of action of allelopathic compounds remains incompletely understood. One of the crucial challenges in allelopathy is to determine the specific mechanism of action of allelochemicals in association with their diverse chemical nature and multiple target sites in plants. The in-depth investigation of the biochemical and physiological changes caused by the allelochemicals on selected weed and crop species is essential to develop an effective weed management strategy based on the allelopathy phenomenon. Plant allelocompounds have different mechanisms of action based on activities such as repellency, growth inhibition, protein denaturation, respiratory impairment, and other effects, depending on the type of botanical compound and weeds (Gawronska and Golisz 2006). To use an appropriate strategy in plant management, it is very important to understand all the existing chemical, biological, and

physical interactions between the plant and the weed (Lengai et al. 2020).

The release of allelochemicals is possible under dry and semi-arid conditions as a result of volatilization, whereby these substances are absorbed as vapors by angiosperm plants, or can be absorbed from the condensate of these vapors in the form of dew, or the condensate can reach the soil and be absorbed by the roots (Kassam et al. 2019). Figure 1 presents the overall processes of allelopathy and the factors influencing allelopathy.

Another mode of action is through leaching by irrigation, dew or precipitation, or plant residues which transport allelopathic substances from the above-ground plant parts to the soil or other plants. The direct source of allelochemical entry into the rhizosphere of the soil is root excretion. The most complex and least understood method is when toxic substances are produced during the decomposition of plant residues or are formed by chemical transformation of starter materials by microorganisms due to the presence of microbial enzymes (Mehdizadeh and Mushtaq 2019). In most cases, allelopathic interference is the result of the concerted action of different compounds. The reactions of plants to different allelochemicals are strongly influenced by the

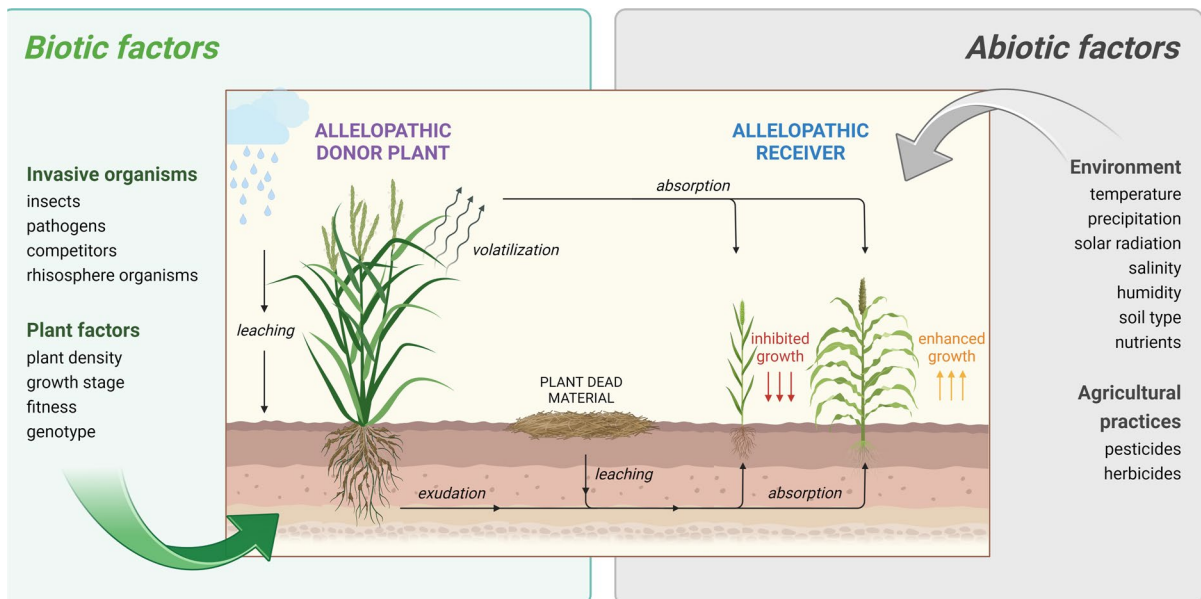


Fig. 1 Scheme of crop-weed interaction including factors of constituting and inhibiting allelopathy (Belz 2007) (created with <https://www.biorender.com/>)

concentration value; at a certain concentration, they inhibit the development of a given species, and at another concentration, they can enhance the development of the same species or another. Additionally, the fate of allelopathic compounds depends on the interactions and kinetics of individual processes occurring, under specific natural conditions, and at a specific location (Mehdizadeh and Mushtaq 2019).

The soil solution plays an important role in allelopathy, there are many compounds considered to be allelopathic, mainly secondary metabolites that are secreted into the rhizosphere and affect the development of plants growing in the vicinity of allelopathic plants (Duke 2010). Many studies describe the multifunctionality of root exudates, e.g. protection against herbivores, change of soil chemical properties, and stimulation of plant growth. It has also been shown that plant secondary metabolites produced inhibit microbially mediated denitrification in the rhizosphere of invasive plants, thereby impacting growth and available nitrogen for the invasive community (Latif et al. 2017). Many potentially allelopathic substances exhibit weak biological activity on plants in the soil due to rapid leaching from the root zone of highly water-soluble compounds and their instability or rapid degradation by microorganism (Mehdizadeh and Mushtaq 2019). Recent research has proven that the synergism of allelopathic substances can increase bioavailability, because of preferential distribution, which leads to increased persistence of allelochemical mixtures in the soil matrix. This relationship has complicated the study of allelopathy, but by the same token, it has also emphasized that it is worthwhile to consider compounds previously excluded as allelochemical on an individual basis because they may, in combination with other constituents, exhibit allelopathic effects (Mehdizadeh and Mushtaq 2019).

For the widespread use of crops and their rhizospheres to control weeds, it is necessary to have a comprehensive knowledge of plant-soil interactions, identify metabolites, and determine their persistence (Mwendwa et al. 2021). Metabolic profiling is a modern tool for assessing the presence and quantity of allelochemicals in the rhizosphere and provides additional insight into the complex interplay between plants and their associated rhizospheric microorganisms. Developing research to investigate the transformation of allelochemicals in soil should pay attention to interactions between metabolites and biotic and

abiotic matrix components that affect transport, degradation, and phytotoxicity.

Phytotoxic allelochemicals include aminophenoxazinones, which are converted from benzoxazinoids produced by wheat as well as in the rhizosphere by soil microbiota (Macías et al. 2019). Benzoxazinoids are unique bioactive metabolites produced by certain members of the *Poaceae* including maize, wheat, rye, and some dicots (Mwendwa et al. 2021). For example, Mwendwa et al. (2021) describe for the first time the production of aminophenoxazinones in Australian soil, demonstrating that weed suppression through allelochemical production can be enhanced under field conditions for some wheat varieties (Latif et al. 2017).

3.1 Impact of allelochemicals on the plant growth regulator system

Allelopathic compounds can cause severe growth disturbances and even lead to complete plant stunting. The expression of specific activity of volatile monoterpenes in blocking mitotic division and inhibiting cell elongation was observed (Kumar et al. 2020). The action of compounds such as coumarin, cineole, and scopoletin results in the formation of cells with altered shapes, abnormally formed nuclei, and highly vacuolated cellular structures (Inderjit and Keating 1999). It was shown that exogenous coumarins can also delay mitosis in onion growth tip cells, and coumarins secreted from *Anthoxanthum odoratum* can inhibit the growth of *Zoysia japonica* seedlings (Chou 1999).

Many studies performed on extracts obtained from different plant species have demonstrated that the toxic effects of allelochemicals are based on delaying seed germination and inhibiting seedling growth. The inhibition of growth can also generate anatomical-morphological deformations at the root tip. Phenolic acids, like coumarins, exhibit similar inhibitory effects on plant growth and induce root morphological deformities (Kumar et al. 2020). Treatment of soybean seedlings with benzoic and cinnamic acids resulted in deformities such as no trichomes, no lateral roots, and a tendency of roots to grow horizontally (Sathishkumar et al. 2020). Other researchers also described the effect of ferulic acid and *p*-coumaric acid as limiting cucumber leaf expansion, *p*-hydroxybenzoic acid and vanillic acid contained in

red bell pepper root exudates as auto toxic—inhibiting the growth of embryonic roots of peppers growing in monoculture crops (Rice 1984).

It was also observed that the inhibitory effect on seedling growth and germination of the phenolic acids (vanillic, ferulic, *p*-coumaric, and *p*-hydroxybenzoic acids) depended more on the type of corn hybrid than the type of acid. The mixture of the investigated acids produces a stronger inhibitory effect than these acids alone. This is consistent with the theory of the synergistic action of these compounds (Parthasarathy et al. 2021). The main indicator revealing the presence of alleloinhibitors in the environment is the inhibition of elongational growth of roots and aerial parts. This negative effect may already be visible during seed swelling—changes leading to anatomical distortions in the seed coat and the seed stocks occur at this point. The result is delayed germination, and the accompanying inhibition of embryonic root elongation which can cause plant death (Liu et al. 2021).

Decreased levels of auxins in tissues can result in a slowing of the growth rate of plants. Monohydroxy phenols, which are cofactors of indoleacetic acid (IAA)-oxidase accelerate the degradation of auxins, while polyphenols and dihydroxy acids have the opposite effect, inhibiting the decarboxylation of IAA, resulting in accelerated growth by the lack of amelioration of this growth enhancer as the plant matures (Bogatek et al. 2005). Adverse effects

of auxins and hydroxamic acids are also possible—because of these acids reduce the ability of auxins to bind to receptor sites on cytoplasmic membranes. Some allelochemicals similar to auxins stimulate ethylene biosynthesis, so this may be a kind of plant indicator for the presence of allelochemicals in the environment (Bogatek et al. 2005).

3.2 Changes in cell membrane permeability

An important change caused by allelochemicals is their effect on the structure and functioning of cytoplasmic membranes (Soltys et al. 2013). Allelochemicals determine the course of plant growth and development by changing the state of cytoplasmic membranes, thereby affecting the course of biochemical and physiological processes in different parts of cells (Fig. 2). Damage to cell membranes affects the entire metabolism and all physiological processes. The consequence of structural changes is the limitation of the functioning of enzymatic proteins that affect intermembrane ion transport, accumulation, and water balance. The hydration of plant tissues affects the state of the stomatal apparatus, thus the process of photosynthesis (Soltys et al. 2013).

Compounds with allelopathic activity may also form molecular assemblies in mitochondrial and chloroplast membranes and modify electron transport therein or decrease cellular adenosine triphosphate

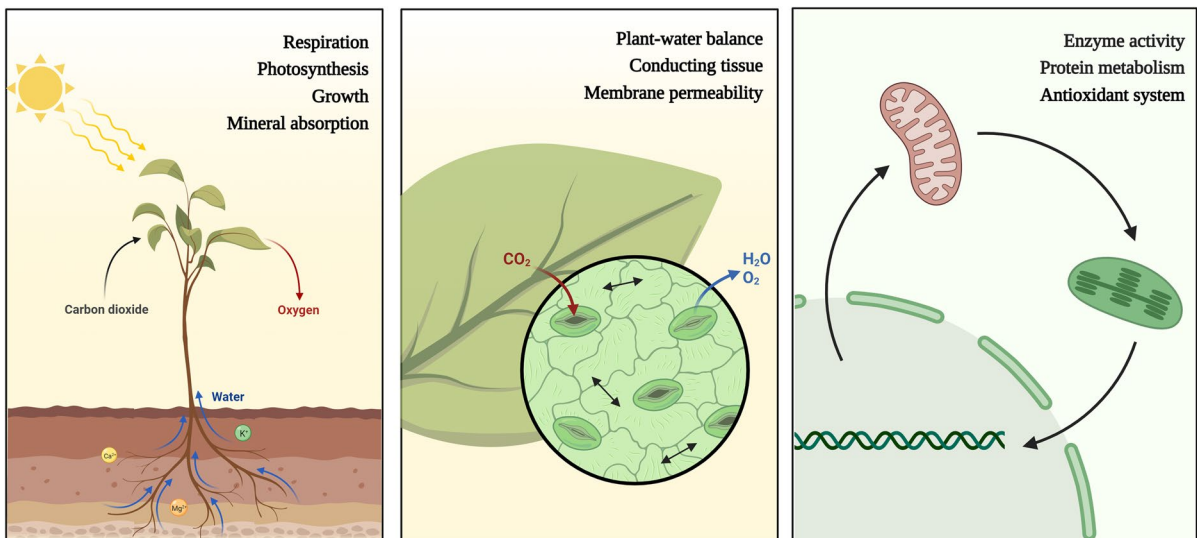


Fig. 2 The effects of allelochemicals on morphological properties and growth rates in plants (created with <https://www.biorender.com/>)

(ATP) formation. Alleloinhibitors can also negatively impact cytoplasmic membrane processes by altering the function of phytohormones by reacting with receptor sites (Cheng and Cheng 2015). Other inhibitors that disintegrate lipid-soluble membrane structures, such as the terpenoids and quinones sorgoleone and juglone, can also be adsorbed on the membrane surface (Gniazdowska et al. 2004).

Scientists researching saponins substantiated their high inhibitory potential against higher plants and microorganisms by observing strong damage mainly in the roots of wheat seedlings (Macías et al. 2019). Saponins interact with the cytoplasmic membranes' constituent elements, proteins, and lipids. As a result of this action, browning of the apical meristem occurs, leading in the next stage to the death of the root system (Rice 1984). The effects of saponins are focused on lowering the activity of membrane enzymes such as nicotinamide adenine dinucleotide (NAD) oxidase and malate dehydrogenase. Interactions of saponins with membrane components are a major cause of saponin-induced damage (de Bertoldi et al. 2009).

Allelocompounds have a significant impact on the water balance in the plant. An example of an allelocompound that affects the water equilibrium of plants is ferulic acid, which has a negative effect on water uptake by cucumbers, beans, and tomato seedlings (Mamolos 2008). Compared to *p*-coumaric acid, it has a stronger inhibitory effect on water uptake by the roots (Schandry and Becker 2020). According to these researchers, plant growth regulators are also involved in the mechanism of action of allelochemicals. *P*-coumaric and ferulic acids, as well as extracts from many weeds with previously known allelopathic properties, caused effects dependent on the concentration of compounds. In the case of higher concentrations, they caused an increase in leaf diffusion resistance and closure of stomata, while at lower concentrations—they decreased the water potential, which was the result of a decrease in the osmotic potential and the pressure potential (Chou 1999).

One of the most significant changes caused by active allelochemicals is their influence on the structure and functioning of cytoplasmic membranes. Allelochemicals determine the progress of plant growth and development by changing the state of cytoplasmic membranes and, consequently, affect the course of biochemical and physiological processes in

different parts of cells (Lengai and Muthomi 2018). When the cell membranes are damaged, there are changes in the entire metabolism and every physiological process. These potent destructive effects are attributed to phenols, which are among the most plentiful and common compounds synthesized in plants that manifest toxic effects even at low concentrations (Mushtaq et al. 2020).

The mechanism of modification of membrane permeability by phenolic compounds is mainly based on the decrease of membrane potential induced by them; the collapse of transmembrane potential in mitochondria induced by salicylic acid is similar. Studies have shown that the permeability of cytoplasmic membranes to electrolytes is mediated by phenolic acids, and that *p*-coumaric and ferulic acids are more effective in membrane disintegration than *p*-hydroxybenzoic and vanillic acids, and that their destructive action is based on peroxidation of membrane lipids (Doblinski et al. 2003). As another example, the toxic activity of benzoic acid and cinnamic acid occurs under the generation of free radicals that damage cytoplasmic membranes. These radicals can be formed, for example, during the oxidative transformation of phenols that occur during cell wall lignification. Allelopathic inhibitors also affect the activity of certain phytohormones that are initiated by receptor sites on membranes by altering their function by reacting with receptor sites (Gniazdowska et al. 2015).

3.3 Influence on water and nutrient uptake

Muscolo et al. (2001), investigated the effects of the concentration and type of phenolic compounds in forest soils with different vegetative cover on *Nipus laricio* seed germination and found that lack of seed germination was strongly correlated with inhibition of glycolysis enzymes and the oxidative pentose phosphate pathway involved in the first stages of seed germination. These kinds of analyses clarify biological interactions in forest soils for natural regeneration and reforestation processes (Muscolo et al. 2001). Allelochemicals have a significant effect on the supply of mineral substances to plants, and their optimal concentration is necessary for the proper growth and development of the plant. Substances contained in decomposing plant residues, extracts, and leachates

may be responsible for altering the mineral content of the plants under study (Muscolo et al. 2001).

Many works have discussed the problem of understanding the mechanism of the effect of phenolic inhibitors on ion uptake by roots of higher plants (Akemo et al. 2000). It was found that as a result of the destruction of the transmembrane electrochemical potential of cytoplasmic membranes, there is an increase in permeability to phenolic acids. The ability of phenolic compounds to inhibit respiration and metabolism in mitochondria, resulting in changes in ATP synthesis, which is responsible for efficient membrane transport should also be considered. The main effects induced by phenolic acids that can alter mineral concentrations in the plant body have been recognized, and their effect depends mainly on the type of ligands in the benzoic ring, for example hydroxyl groups can mitigate the inhibitory effect. Phenolic acids can produce effects characterized by direct action—modifying the rate of uptake, as well as long-term, for instance changing the concentration of ions in plant tissues (Głąb et al. 2017). Based on many literature items, it can be assumed that most phenolic acids decrease the level of essential elements in plant materials except chlorogenic acid, which in the case of tissues of the plant *Amaranthus retroflexus* caused a decrease in the level of phosphorus, increased nitrogen, and had no effect on the level of potassium. Salicylic acid also negatively affects ion uptake by inhibiting barley roots' absorption of potassium and phosphorus ions. Benzoic and cinnamic acids cause growth inhibition of soybean (*Glycine max*) seedlings because of disturbances in ion uptake and transport in the plant; the interferences are additionally accompanied by morphological distortion of the roots. The rate of ion uptake differed depending on the cinnamic acid concentration in the rhizosphere soil. For phosphate ions, inhibition occurred at higher concentrations, and acid toxicity increased with decreasing soil pH (Hoang Anh et al. 2021).

3.4 Impairment in the antioxidant system and effect on plant photosynthesis

There is a strong correlation between respiration and patterning processes, so compounds that cause disruptions in respiration processes also have a significant impact on the growth process. These effects are mainly observed in mitochondrial

metabolism—specifically in the Krebs cycle and respiratory chain transformations (Kumar et al. 2020). Studies leading to a comparison of the activity of individual allelochemicals belonging to different classes on the respiration rate of soybean cotyledons described that due to the small size of α -pinene and cinnamic acid particles, they more efficiently penetrated the tissues and thus accelerated the damage to mitochondria, compared to quercetin and juglone (Peñuelas et al. 1996). Glycosides also negatively affect the respiration process. Resin glycosides were found to inhibit membrane ATPase in *Ipomea tricolor* (Calera et al. 1995).

Disturbances in the photosynthesis process caused by allelocompounds may be one of the reasons for the inhibitory effects on plant growth. Among phenolic acids, the greatest toxicity is revealed by salicylic acid, but in general phenolic compounds have a weak effect on the photosynthesis process (Latif et al. 2017). Phenolic compounds can block the release of oxygen by chloroplasts, but high concentrations are required to induce significant changes. Based on studies conducted on a cell suspension of *Abutilon theophrasti*, it was shown that at the highest tested concentrations, vanillic and ferulic acid inhibited photosynthesis and protein synthesis, respectively, while chlorogenic and *p*-coumaric acids did not inhibit any of the physiological processes (Latif et al. 2017). Disturbances in photosynthesis can also be caused by short-chain organic acids, sesquiterpene lactones, indole alkaloids, or flavonoids. For example, artemisinin, one of the sesquiterpene lactones, is an extremely active inhibitor of photosynthesis because it reduces this process even at low concentrations. The effect of allelopathic substances on photosynthesis is also reflected as a change in chloroplast activity, which is particularly strong for the quinone inhibitors sorgoleone and juglone. Sorgoleone detected in sorghum (*Sorghum bicolor*) already at low concentrations induced a 50% inhibition of oxygen secretion by *Glycine max* leaves (Głąb et al. 2017).

3.5 Effect on the functions and activities of enzymes

Many allelochemicals are known that can be both inhibitory and activating on enzymatic systems. A reduction in protein synthesis by phenols is very common, as well as changes in the metabolism of porphyrin compounds caused by phenolic acids. This results

in the inhibition of chlorophyll and hemoglobin synthesis, which is necessary for root papilla formation by legumes (Bogatek et al. 2005). Based on an experiment conducted on a research material consisting of cucumber stems and leaves, cultivated on a medium containing high amounts of phenolic compounds, it was found that the activity of IAA oxidase was higher than in the plants cultivated on media with a low content of these compounds. On the other hand, the results of other studies show that phenolic compounds, mostly phenol acids, stimulate the increase of guaiacol peroxidase enzyme activity in white clover roots (Bogatek et al. 2005).

The fundamental effect of allelopathic compounds on the cell membrane is based on the modification of the transmembrane barrier, resulting in morphological and physiological changes that inhibit growth and development (Mushtaq et al. 2020). Allelochemicals generally affect cellular processes but do not damage cellular organelles. The direct visible effects of their phytotoxic properties are for example, swollen seeds, rotting or swollen root tips, an absence of root hairs, the reduced extension of roots and twisting of their axis, diminished dry biomass accumulation, repressed germination rate and reduced reproductive potential (Mushtaq et al. 2020).

4 Factors affecting the release of allelochemicals

The most significant challenge associated with allelopathic weed control is the low concentration of allelochemicals in the source plants and the difficulty in synthesizing these compounds for large-scale commercial use. A proposal for solving this problem is to use stress factors, which generally potentiate the synthesis of allelocompounds in plants. In addition, biotic and abiotic factors influence the expression of allelopathy and are, therefore, a tool to manipulate the persistence, concentration, and fate of allelopathic compounds in the environment (Inderjit and Keating 1999). Stress-induced stimuli received by the plant at the cellular level follow different perceptual or signal transduction pathways, resulting in direct metabolic response and activation of gene expression. Reactions usually activated under the influence of environmental signals include the formation of enzymes and the synthesis of stress proteins, hormones, and stress metabolites, subject to feedback control (Scavo and

Mauromicale 2021). In addition, it has been observed that allelochemicals present in the vicinity of plant roots or induced by neighboring plants can induce secondary oxidative stress on plants. These phenomena increase reactive oxygen species, activating the cellular antioxidant system and disrupting hormonal balance (Maqbool and Abdul 2013). Allelopathic effects can result from the direct release of chemical compounds from the donor plant and from the induction of the release of biologically active compounds by a third species. These phenomena can also be indirectly influenced by degraded or transformed products of released compounds resulting from abiotic and biotic influences on soil or water (Inderjit and Keating 1999).

Environmental factors such as climate, soil structure, soil nutrient content, water properties (physical, chemical, and biological), and agricultural practices are responsible for the concentration of allelochemicals in the plant (Maqbool and Abdul 2013). Under stress conditions, plants produce allelochemicals consisting mainly of phenolic acids and terpenoids. Allelopathic activity under dry soil conditions is higher than in well-irrigated areas for plant species such as cassava (*Manihot esculenta* Crantz), sorghum (*Sorghum bicolor*), sunflower (*Tithonia diversifolia*) and walnut (*Cyperus rotundus*). Under drought conditions elevated levels of cyanogenic glycosides were recorded for the species mentioned above and increased amounts of ferulic acid in wheat (Maqbool and Abdul 2013). Additionally, an increase in barley autotoxicity under drought conditions has been observed, and rice responses to drought and salinity have also been demonstrated through the production of momilactones A and B as a defense mechanism (Scavo and Mauromicale 2021). An increase in the production of phenolic compounds has been noted as a result of changes in soil characteristics, such as conductivity, pH, organic carbon content, and nutrient content (Nornasuha and Ismail 2017). The secretion of phenolics influences nutrient availability, the dynamics of organic matter, and nitrogen mineralization. For example, scopoletin and chlorogenic acid concentrations increased several-fold in all tobacco and sunflower plants under potassium, sulfur, and nitrogen-deficient conditions. Similarly, scopoletin was shown to help tobacco plants survive in soil deficient in boron, magnesium, calcium, and

phosphorus (Maqbool and Abdul 2013). Zobel and Clarke (1999) had already observed increased synthesis of allelochemicals under high heavy metal content in the soil. Other researchers later confirmed that severe metal stress increased momilactone B levels in rice crops (Kato-Noguchi 2009).

In response to pathogenic organisms, plants activate defense mechanisms that increase the production of secondary metabolites with defensive effects (Nornasuha and Ismail 2017). Disposal of plant residues can generate biotic stress for newly growing plants. The microorganisms use energy, some mineral elements, water, and oxygen during the decomposition of residues, which, if insufficient in the soil environment, would result in competition for limited resources. Some products of decomposed residues are of nutritional value for new vegetation others are phytotoxic and interfere with soil microbes (Gawronska and Golisz 2006). Another example of biotic stress is competition in plants living in unsuitable conditions competing for the resources necessary for growth. Harmful allelopathic interference can also occur between plants of the same species. The occurrence of autointoxication poses a problem when transplanting fruit trees in orchards, shrubs, and perennial plantations, as well as field plants and crops that need to be transplanted every year (Gawronska and Golisz 2006).

In a complex ecosystem, different stress factors act synergistically to increase allelochemical synthesis. This causes difficulties in manipulating stress induction to obtain adequate amounts of compounds with the allelopathic potential to use for bioherbicide production (Scavo and Mauromicale 2021). However, tremendous advances in molecular biology, metabolomics, genomics, and proteomics, as well as modern biotechnological techniques, have contributed to a better understanding of such complex interactions. At the same time, it is possible to link genes involved in the production of secondary metabolites and modify their composition by employing genomic approaches and genetic engineering. Allelopathic interactions induced by biotic and abiotic stresses trigger processes at all levels of trophic relationships, which can be used to develop biocontrol measures in organic farming and also in ecosystem management (Gawronska and Golisz 2006).

5 Allelochemicals as plant secondary metabolites

5.1 Nitrogen-containing compounds

Alkaloids are plant-derived heterocyclic compounds and are among the largest group of secondary metabolites, with over 27,000 currently listed in the Dictionary of Natural Products (Parthasarathy et al. 2021). Alkaloids are mainly amino acid derivatives but can also be synthesized via terpenoids or formed from polyketide pathways (Macías et al. 2019). They can be differentiated based on their biosynthetic origin into several groups: indole alkaloids derived from tryptophan, pyrrolizidine alkaloids from ornithine or arginine, and quinolizidine alkaloids from lysine (Latif et al. 2017). They are synthesized in the cytoplasm, vesicles, or chloroplasts but can also be stored in vacuoles due to their water-soluble abilities (Macías et al. 2019). The purine alkaloid caffeine causes autotoxicity in coffee and tea plantations, whereas gramine and nicotine affect seed germination and shoot growth (Bachheti et al. 2020). The activity of these compounds occurs in relatively high concentrations (>0.1%), compared to phenolic compounds, which are toxic already in concentrations of 10–200 ppm (Yoneyama and Natsume 2010). Alkaloids induce plant growth inhibition by interfering with DNA, causing changes in enzyme activity, protein metabolism, and cytoplasmic membrane integrity, amongst other things. This is confirmed, for example, by studies in which quinolizidine alkaloids produced by legumes, such as lupanine and spartenin, impaired membrane permeability and inhibited protein synthesis. Plant alkaloids are widely prevalent in four plant families, including *Asteraceae*, *Apocynaceae*, *Boraginaceae*, and *Fabaceae* (Latif et al. 2017).

The production of plant alkaloids with significant allelopathic effects is still fully unconfirmed, however, compounds such as morphine, berberine, ergotamine, allyl isothiocyanate, quinine, and colchicine have been confirmed to exhibit phytotoxicity, inhibit germination and/or seedling growth of neighboring plants. In some experiments, scopolamine and hyoscyamine were isolated from the soil where colcora (*Datura stramonium*) was growing and showed an inhibitory effect on *Helianthus annuus* seedlings that lasted for eight months (Haig 2008). A research study was also conducted in which the alkaloid fraction of

Crotalaria retusa was collected and tested at various concentrations for allelopathic potential in *Phaseolus vulgaris*. With increasing concentration, allelochemicals inhibited bean seed germination through induced oxidative stress (Bachheti et al. 2020). The chemical structures of selected compounds with allelopathic potential are presented in Fig. 3.

Benzoxazinoids, which show significant allelopathic potential, are another group of compounds that are abundant in the world's largest field crop species such as rye, wheat, corn, and rice (Hussain et al. 2022). They have been thoroughly tested

for allelopathic efficacy and phytotoxicity on weeds. Various benzoxazinoids and hydroxamic acids, including benzoxazolin-2(3H)-one (BOA), benzoxazinones 2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one (DIMBOA), 2-hydroxy-7-methoxy-1,4-benzoxazin-3-one (HMBOA), 2-hydroxy-1,4-benzoxazin-3-one (HBOA), 6-methoxy-benzoxazolin-2-one (MBOA) and 2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one (DIBOA), are synthesized in cereals and released from the plant tissues and residues by decomposition and through root exudation (from root hairs or secondary roots)

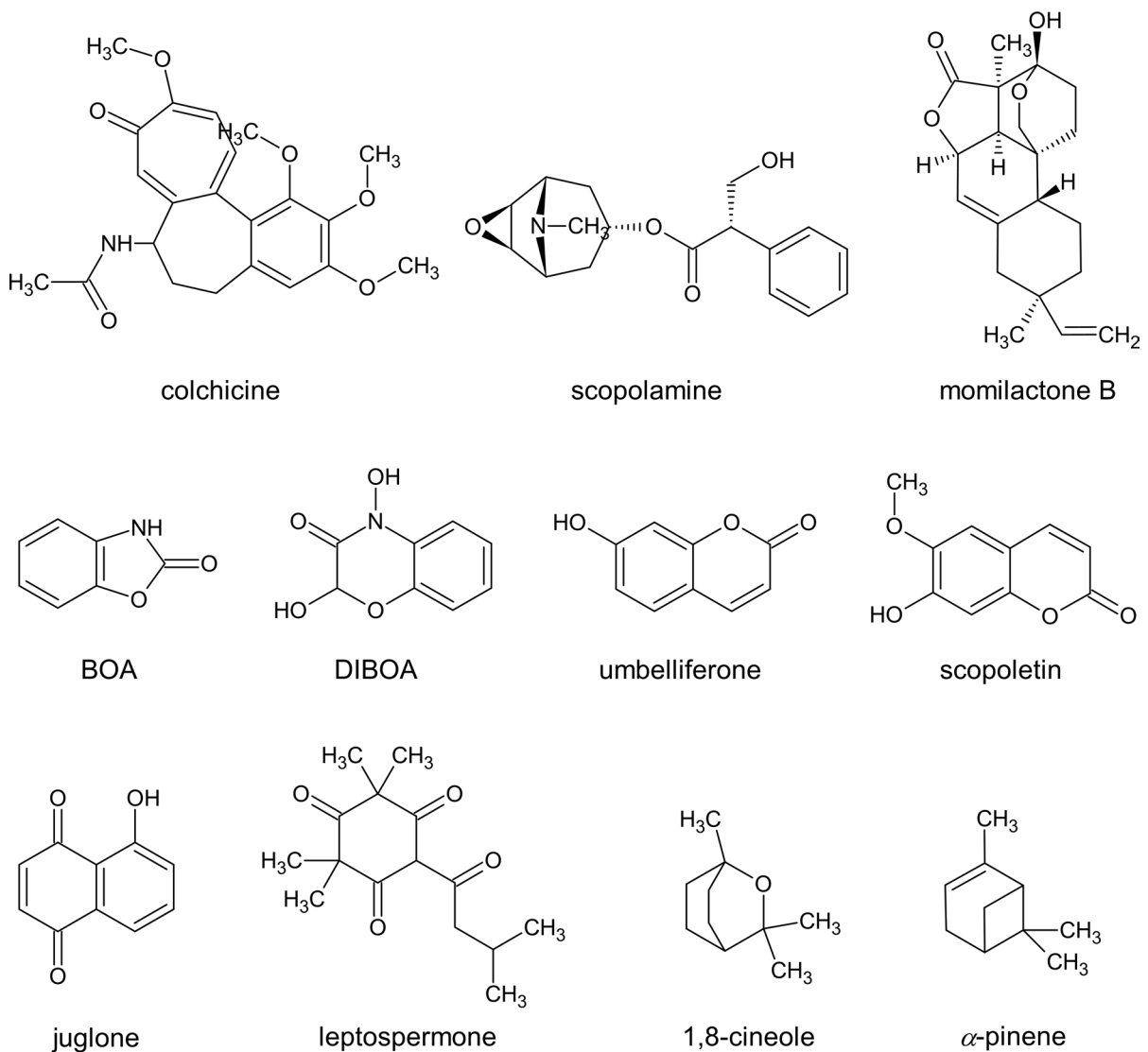


Fig. 3 Examples of natural products with allelopathic actions

into the surrounding soil solution (Reiss et al. 2018). It has been shown that after production and release, they undergo physicochemical and microbiological changes, thus causing changes in phytotoxicity mediated by microorganisms (Hussain et al. 2022).

Benzoxazinones are stored in the glucosidic form in vacuoles, however, as a result, external triggers are released into the cytoplasm, and they are hydrolyzed by the β -glucosidases increasing their reactivity and biological activity (Gawronska and Golisz 2006). The resulting unstable benzoxazinone aglucones (DIBOA and DIMBOA) are toxic, and their benzoxazinone degradation products (MBOA and BOA) are considered to be less bioactive than the starting molecules. Despite this, it has been shown that the glucosides of DIBOA and DIMBOA with their respective aglycones and degradation products, suppress weeds such as barnyard grass, crabgrass, or redroot pigweed (Gawronska and Golisz 2006).

Allelochemicals from various wheat genotypes have also been shown to mainly inhibit the growth of various weed species, including *Bromus japonicus*, *Chenopodium album*, *Portulaca oleraceae*, *Avena fatua*, and *Lolium rigidum* (Hussain et al. 2022). The soil microflora is responsible for the transformation of benzoxazinones into more potent bioherbicide

metabolites. Benzoxazinones may be useful as weed control agents due to their phytotoxicity, specific activity, and limited soil persistence. Such research can be used to develop modern benzoxazinone-rich wheat breeding for sustainable weed control programs (Hussain et al. 2022).

5.2 Phenolic compounds

Plant phenolics are a diverse group of organic compounds, their common feature consists of an aromatic ring possessing at least one hydroxyl group. Phenolic compounds are synthesized via the phenylpropanoid and shikimic acid pathways, whereas the combination of the shikimate pathway with the mevalonate pathway leads to the synthesis of flavonoids. These processes are all presented in Fig. 4. Phenolic compounds can be generally classified into phenolic acids, flavonoids, coumarins, lignins, tannins, and stilbenes (Latif et al. 2017). Phenolic compounds can exist in free form, conjugated with sugars or proteins, as esters, and by polymerization and condensation from tannins, lignans, lignin, cutin, and suberin (Borrelli and Trono 2016).

Benzoic and cinnamic acid derivatives are the most common plant-originated allelochemicals,

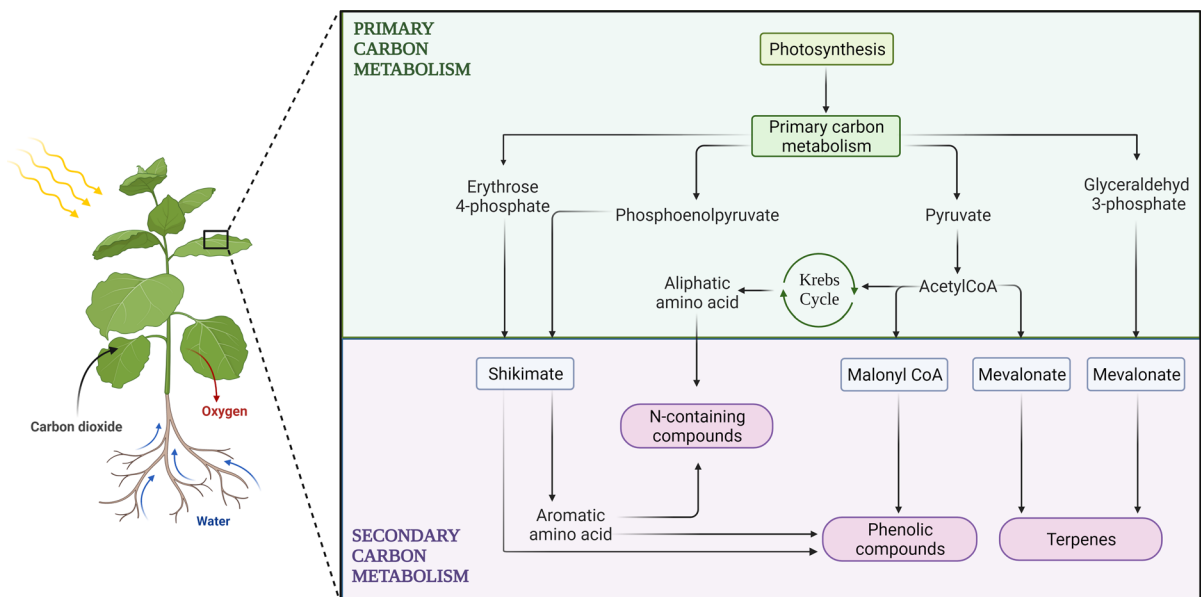
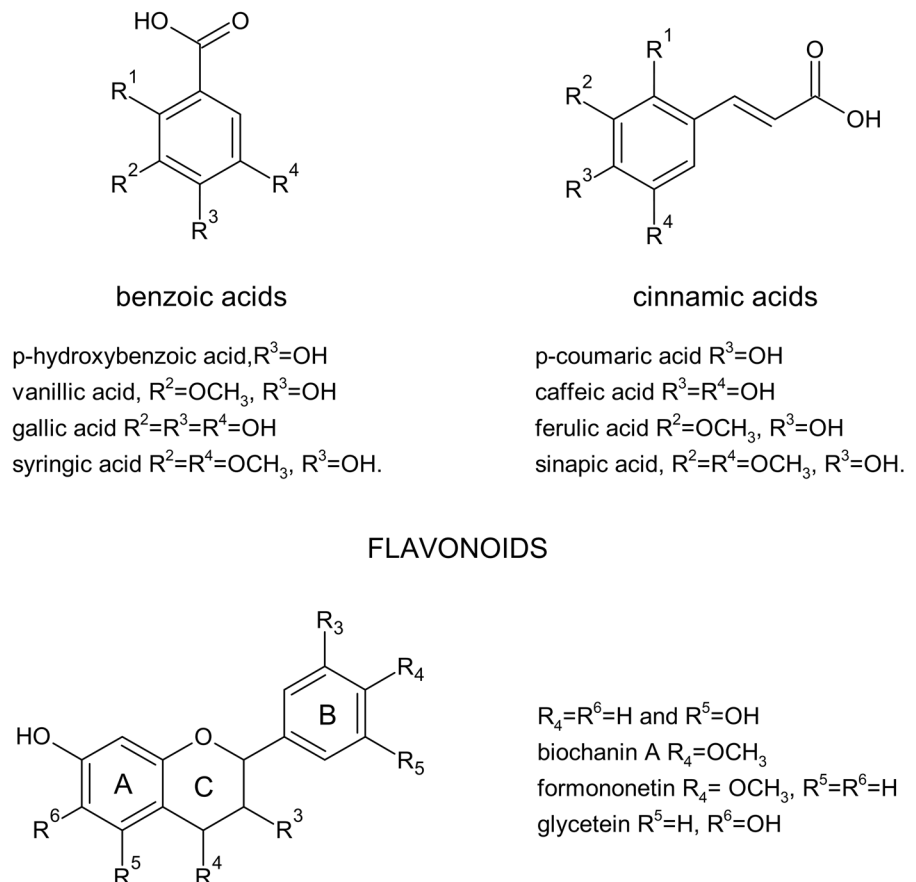


Fig. 4 General scheme of the relationships between primary metabolism and the major pathways for the synthesis of secondary metabolites (created with <https://www.biorender.com/>)

for example, *p*-hydroxybenzoic acid, salicylic acid, gallic acid, vanillic acid, *p*-coumaric acid, caffeic acid, ferulic acid, and chlorogenic acid, which structures are presented in Fig. 5 (Yoneyama and Natsume 2013). Among the cinnamic acids, caffeic acid and its esterified derivatives are the most abundant in fruit, whereas derivatives of ferulic acid are the most abundant in cereal grains. Flavonoids are among the most powerful antioxidants that have been obtained from plants, and their effects are due to the presence of hydroxyl groups in positions 3' and 4' of ring B, which participate in electron delocalization and stabilize the radical that is formed, and of a double bond between the C2 and C3 carbons in ring C, together with a carbonyl group at the C4 carbon, which makes delocalization of an electron from ring B possible, (Fig. 5) (Borrelli and Trono 2016).

The mechanism of allelopathy associated with phenolic compounds includes interfering with hormone activity, membrane permeability, photosynthesis, respiration, and synthesis of organic compounds in susceptible plants (Latif et al. 2017). Free phenolic compounds affect plant growth because they accumulate in rhizosphere soils, thereby influencing the accumulation and availability of soil nutrients (Li et al. 2010). Examples are the main allelochemicals in the rhizosphere soil of *Ageratum conyzoides* L., which were isolated and identified as *p*-coumaric acid, gallic acid, ferulic acid, *p*-hydroxybenzoic acid, and anisic acid, with allelopathic interference on rice (*Oryza sativa*). Research by Batish et al. (2009) showed that root exudates and residues of *A. conyzoides* released inhibitory substances in the soil rhizosphere, and these phytotoxins negatively affected rice growth. The phenolic

Fig. 5 Structures of phenolic compounds with allelopathic potential (Borrelli and Trono 2016)



content of the phytotoxins isolated from the soil solution was nearly six times higher compared to the control soil solution (Batish et al. 2009).

The allelopathic effect is the strongest when a combination of multiple phenolic compounds are present. For example, one study investigated the effect of an aqueous extract of *Delonix regia* on the growth of lettuce (*Lactuca sativa*) and Chinese cabbage (*Brassica chinensis*) (Li et al. 2010). Chlorogenic acid, protocatechuic acid, gallic acid, 3,4-dihydroxybenzaldehyde, *p*-hydroxybenzoic acid, caffeic acid, and 3,5-dinitrobenzoic acid were identified in this extract. This combination of compounds with allelopathic potential inhibited the growth of the neighboring plant, and this effect increased with increasing concentrations of these compounds (Li et al. 2010).

Some of the potential phenolic allelochemicals were identified in the leachates of bark, fresh leaves, and leaf litter of *Eucalyptus tereticornis*, *E. camaldulensis*, *E. polycarpa*, and *E. microtheca*. Investigations showed the presence of *p*-coumaric, gallic, gentisic, *p*-hydroxybenzoic, syringic, and vanillic acids and catechol, which have harmful effects on the crops in the ecosystem, for example, black gram (*Phaseolus mungo* L.), resulting in the reduction and delaying of germination, mortality of seedling and reduction in growth and yield (Li et al. 2010). Other reports are available that detail the *Eucalyptus* species allelopathic effect. The allelopathic activity was investigated against seed germination of *Abutilon theophrasti*, *Asclepias syriaca*, and *Chenopodium album*. Crude wheat and corn straw extracts compared to fermented extracts show more inhibition of seed germination and seedling growth of *Abutilon theophrasti*, *Asclepias syriaca*, and *Chenopodium album* (Bachheti et al. 2020). It is also worth noting that some researchers observed that the application of a bur cucumber seed extract and its phenolic chemical (2-linoleoyl glycerol) triggers abscisic, salicylic, and jasmonic acid accumulation, and inhibits the gibberellin pathway, so seed germination of lettuce will be halted (Kumar et al. 2020). A large number of reports on the discovery of phenolic allelochemicals from plants testifies to the huge and almost unexploited reservoir of compounds that can potentially be used for pest and weed control in the field of agricultural production. Accurate identification and quantitative analysis of allelopathic phenolic compounds are the basis for developing toxicologically benign weed

management and pest control tools with high nutritional value (Kumar et al. 2020).

Coumarins and their glucosides are abundant and commonly present phytochemicals in plants in particular families *Apiaceae*, *Rutaceae*, *Asteraceae*, and *Fabaceae* (Bachheti et al. 2020). A C7 hydroxyl group in the coumarin structure seems to contribute significantly to the herbicidal activity of this family of compounds, therefore accordingly, 7-hydroxycoumarins, such as umbelliferone, esculetin, and scopoletin, (Fig. 3) have received interest as eco-friendly herbicides and are known for their allelopathic effect (Galán-Pérez et al. 2022).

As for the apparent additive effect already noted among the phenolic acids, coumarin effects can similarly be enhanced by the presence of phenolic acid (Haig 2008). For example, Korableva et al. (1969) report that scopoletin is more effective as a growth retardant when used in combination with caffeic acid than when used alone, and Einhellig (1996) reports that a combination of coumarin (umbelliferone), phenolic acid (salicylic acid), and flavonol (rutin) also possesses a phytotoxic effect in the mixture. While the phenolic acids do not show evidence of being able to influence cell division, compounds such as scopoletin and coumarin have been reported to have an effect in decreasing mitosis, and also inhibiting certain enzyme actions (Haig 2008). Scientists after most in-depth analysis observed that scopoletin, one of the most common coumarins in higher plants, displayed strong phytotoxicity on *Arabidopsis thaliana* seedlings, and showed its herbicidal activity towards the parasitic weed *Orobancha crenata* (Galán-Pérez et al. 2022).

Misra et al. (2020), in their carefully designed study, employed non-targeted metabolomics to investigate the short-term metabolic changes induced in wheat seedlings by the allelochemical umbelliferone. The study clearly showed the system-wide metabolomic changes in wheat seedlings in response to umbelliferone treatment. The approach was novel due to the initial short-term experiment using sub-lethal concentrations. This non-targeted metabolomics approach allowed the identification of system-wide metabolic responses activated by the plants to deal with this phytotoxic compound. It has been shown that umbelliferone induced the dysregulation of metabolites involved in the shikimate pathways, as well as in tryptophan and tryptamine metabolism.

This experiment provides new insights into the early response of plants to this specialized allelopathic metabolite and can inform the design of new organic herbicide approaches (Misra et al. 2020).

Juglone (5-hydroxy-1,4-naphthalenedione), (Fig. 3) is a phenolic compound well known to have a negative impact on the growth of other plants, produced by the black walnut (*Juglans nigra* L.). Juglone is a strong inhibitor of hydroxyphenylpyruvate dioxygenase (HPPD), the key enzyme in plastoquinone biosynthesis, and also inhibits photosynthetic and respiratory electron transport systems (Yoneyama and Natsume 2013).

Leptospermone (1-hydroxy-2-isovaleryl-4,4,6,6-tetramethyl cyclohexen-3,5-dione), (Fig. 3), is a natural triketone produced by the roots of the bottlebrush (*Callistemon citrinus* Curtis) and its herbicidal activity is due to its inhibition of *p*-hydroxyphenylpyruvate dioxygenase. These disorders lead to disruption in carotenoid biosynthesis and loss of chlorophyll. Its herbicidal action at high doses excludes commercial development. However, the structure of leptospermone was used as a basis for developing synthetic analogs applied for the control of broadleaved weeds in maize, for example (Soltys et al. 2013). Dayan et al. (2011) draw attention to manuka oil, with the principal active ingredient leptospermone which can be used to potentiate the herbicidal activity of other herbicidal essential oils. Manuka oil (1%) applied as a post-emergence spray, significantly decreased the growth and dry weight of redroot pigweed, barnyard grass, velvetleaf, and hairy crabgrass. Scientists have proven that manuka oil can be used to potentiate the herbicidal activity of other herbicidal essential oils due to additive or synergistic action. This kind of application poses another possibility of usage for this allelopathic compound in its natural form without chemical modification of the structure (Soltys et al. 2013).

5.3 Terpenes

Terpenoids are classified based on the number of isoprene units in their carbon skeleton, e.g. monoterpenes, sesquiterpenes, diterpenes, sesterpenes, and triterpenes (Nair et al. 2022). Two distinct pathways are involved in the production of the basic isoprene units—*isopentenyl diphosphate* (IDP) and *dimethylallyl diphosphate* (DMADP)—required for terpenoid

synthesis. In plastids, the methylerythritol phosphate (MEP) pathway, while in the cytosol, endoplasmic reticulum, and peroxisomes the mevalonic acid (MVA) pathway takes place, as shown in Fig. 4 (Corso et al. 2021). Terpenoids have multiple biological activities in plants as photoprotective agents, mediators of polysaccharide assembly, reproductive hormones, allelochemicals, and agents in communication and defense. Several studies confirm the allelopathic nature of terpenoids, causing inhibitory and autotoxic effects on seedling germination and growth. Such effects are due to characteristic interactions such as disruption of ATP formation and endocrine activity, complexation with proteins, and obstruction of respiration (Bachheti et al. 2020). Considering these properties terpenoids have a high potential as pollinator attractants, in the defense of plants against herbivores and microbial pathogens (Borrelli and Trono 2016).

Monoterpenes, such as 1,4-cineole and 1,8-cineole, are the main constituents of plant essential oils and are widely known for their strong inhibitory effects on plant growth and seedling germination (Latif et al. 2017). Monoterpenes and sesquiterpenes have been quite well characterized in terms of their phytotoxic potential. For example, the sesquiterpene *b*-caryophyllene is present in numerous plant volatiles and has an inhibitory effect on germination and seedling growth of *Brassica napus* L. and *Raphanus sativus* L. even at very low concentrations (Latif et al. 2017). However, in other studies, allelopathic monoterpenes such as *p*-menth-2-en-1-ols thymol, carvacrol, 1,8-cineole, α -pinene, and β -pinene were isolated from *Eucalyptus* species. Furthermore, sesquiterpenes such as spathulenol and α -, β -, and γ -eudesmols were detected in *Eucalyptus* in other experiments (Bachheti et al. 2020).

Asteraceae plants such as asters, daisies, and sunflowers are another example of a natural source of allelopathic sesquiterpenes and sesquiterpene lactones (Araújo et al. 2021). Araújo et al. (2021) show that monoterpenes can act by inhibiting the enzyme asparagine synthase, thus preventing growth. Their action may also include impairing mitochondrial cell respiration of organelles and a slow release of proteins in the plasma membrane.

Momilactones belong to a group of naturally occurring diterpenes known as (*9* β -H)-pimaranes, which are characterized by a β -orientation of the

proton on carbon-9 of the pimarane skeleton (Yoneyama and Natsume 2013). Momilactone B (Fig. 3) has allelopathic properties, such as antifungal activity against the pathogen *Piricularia oryzae*, which causes a devastating disease leading to 10–30% loss in total rice yields, as well as production losses in wheat, barley and millet crops (Zhao et al. 2018). Momilactone B was found in shoots and roots of rice plants over their entire life cycle and its highest level in this part of plants at the day of flowering initiation was 245 and 64.1 nmol g⁻¹ fresh weight, respectively. When converted to 1 kg of rice shoots and roots, this plant mass was found to be able to release 245 and 64.1 μmol of momilactone B into the soil or neighboring environment by decomposition of their residues (Kato-noguchi and Ino 2005). Momilactone B inhibits the growth of typical rice weeds like *Echinochloa crus-galli* and *E. colonum* at concentrations greater than 1 μmol/L (Amb and Ahluwalia 2016) so this concentration may be sufficient to cause growth inhibition of their neighboring or successional plants (Kato-noguchi and Ino 2005). This evidence supports the idea that allelochemicals can be important tools for weed management, helping to address the challenges of environmental pollution and herbicide resistance.

6 Allelopathic potential in the world's most important crop cultivation

Some crop accessions: wheat (*Triticum* sp.), rye (*Secale cereale*), maize (*Zea mays*), rice (*Oryza sativa*), and sorghum (*Sorghum bicolor*), have been shown to possess strong allelopathic potential against the growth of certain weed species (Schandry and Becker 2020). However, the exploitation of the potential of these crops in agriculture depends on the stability of the allelochemicals and their environmental fate, as well as their presence in biologically active concentrations. The role of the biotic soil environment is fundamental in assessing allelopathic traits of crops for agricultural strategies such as weed management (Schandry and Becker 2020).

Implementation of suitable weed management practices is critical in crop production to minimize competition for water, nutrients, space, and light between weeds and economically important crops. Over the past several years attempts have been made

to enhance the allelopathic properties of crops by variety selection and conventional breeding (Mohammadi 2013). Allelopathy is a cost-effective and environment-friendly approach to replacing synthetic herbicides therefore, keeping in mind the role of this phenomenon in weed management, many scientists are involved in designing strategies to manipulate the allelopathic traits of globally cultivated crops. Several studies support the thesis that many crops exhibit allelopathic effects relative to other crops grown simultaneously or downstream. Therefore, many crops have been considered for allelopathic activity against other plants or weeds (Chung et al. 2018). Sustainable food security requires abundant yields from a limited land area. A major challenge is maximizing crop productivity under changing climatic conditions to meet global food security challenges.

6.1 Rice (*Oryza sativa* L.)

Of the species with allelopathic character, special mention should be made of rice (*Oryza sativa* L.)—one of the most important crops worldwide, with more than 1.5×10^8 hm² of land being cultivated for its production (Amb and Ahluwalia 2016). Although rice is cultivated on a massive scale—globally, rice provides about 20% of the caloric intake for more than 50% of the world's population—its yields are at risk of significant losses due to disease, pests, and weeds. To minimize losses, three million tons of herbicides are currently used annually worldwide to control paddy weeds in agricultural systems (Chung et al. 2006). Considering that rice is a staple food for most of the world's population, controlling weeds in rice agriculture is of utmost importance. Extensive use of herbicides in rice cultivation has led to the development of herbicide resistance in a wide range of weeds, thus in countries such as China, Korea, Japan, the USA, and India, extensive research has been initiated to exploit the allelopathic potential of this plant (Mushtaq et al. 2020).

Fields of rice have ecotones that encompass aquatic habitats as well as drylands and therefore harbor biodiverse plant communities (Chung et al. 2006). Additionally, the paddy field ecosystem maintains nutrient recycling, trophic structure balance, and water recharge. The ability of rice to grow in water has been used as part of weed control, as weeds are less likely in this medium, but growing rice in water

is a labor-intensive process and irrigation measures are becoming scarce with time (Mushtaq et al. 2020). Several rice varieties are known to release biocidal allelochemical compounds which might affect microbial and pathogenic diversity and soil characteristics (Mushtaq et al. 2020). Since these interactions may be positive, it is advantageous to use this as an effective contributor to a sustainable and eco-friendly system (Chung et al. 2006).

Based on many studies, researchers have concluded that plants having higher yield potential, strong competitive ability against weeds, adequate plant height and sufficient leaf area may have heightened allelopathic potential (Mushtaq et al. 2020). Rice cultivars and lines have been analyzed for the effects of this crop on the growth of common weeds. A wide range of chemical compounds produced by this plant have been isolated, including momilactone A and B, resorcinols, cyclohexanones, flavones, benzoxazolinones, and glycoside derivatives. Secondary plant metabolites such as phenols, coumarins, terpenoids, steroids, alkaloids, and indoles have also been identified (Gniazdowska 2007).

Several reports confirm a key role in rice allelopathic activity of momilactone A and B, which are secreted by rice roots into the rhizosphere over the entire life cycle. Allelopathic varieties of these plants can release up to 2–3 µg of momilactone B per day (Soltys et al. 2013). These allelochemicals inhibited the growth of typical weeds in rice, e.g. awnless barnyard grass (*Echinochloa colona* Link.). In addition the phytotoxic abilities of momilactones were also demonstrated on livid pigweed (*Amaranthus lividus* L.), hairy crabgrass, and annual bluegrass (*Poa annua* L.) at specific concentrations (Soltys et al. 2013).

Momilactones were first isolated as growth inhibitors, but were later, also found as phytoalexins (Soltys et al. 2013). Momilactone A and B, considered unique to rice, are diterpenoid phytoalexins, and are antimicrobial secondary metabolites that are produced in response to signaling molecules termed biotic elicitors. Recently, these compounds have also been found in a taxonomically distinct plant, the moss (*Hypnum plumaeforme* Wils.), but although they have a proven ability to inhibit plant growth, the mechanism of their action in plants is still unrecognized (Soltys et al. 2013).

Diterpenoid momilactones are an example of natural compounds for which correlative biochemical

evidence for a role in allelopathy has been obtained. Researchers used reverse genetics, using knock-out of the respective diterpene synthases (copalyl diphosphate synthase 4 (OsCPS4) and kaurene-like synthase 4 (OsKSL4)), aimed at providing evidence that rice momilactones are responsible for allelopathy, mainly inhibiting the growth of the widespread rice weed *Echinochloa crus-galli*. These conclusions furnish a molecular target for breeding and metabolic engineering and the intriguing possibility of momilactone biosynthesis in situ-produced herbicides in rice crops (Xu et al. 2012).

Under field conditions, almost all rice cultivars indicate allelopathic potential against ducksalad, barnyard grass, redstem, and monochoria, which represent real rice–weed interaction and show more than 40% inhibition of spinach growth (Mushtaq et al. 2020). The finding that more than one allelochemical is responsible for the allelopathic effect is based on laboratory and field testing showing that rice cultivars can inhibit both monocotyledonous and dicotyledonous weeds (Mushtaq et al. 2020). Many allelochemicals were isolated from the roots of different rice cultivars, but none of these was able to break the growth effects of weeds alone. Further experiments made between weed plants and rice, and also the research of more genetic and morphological characteristics using more rice varieties are needed (Ahn et al. 2005). The combination of plant allelopathy with existing agrotechnical practices can be an ecological approach to increase agricultural yields through sustainable weed management. Understanding the factors influencing allelochemical production in rice and the mechanisms of their phytotoxic effects can help develop novel weed control tactics while enabling farmers to manage weeds in an environmentally friendly manner (Rahaman et al. 2022).

6.2 Wheat (*Triticum aestivum* L.)

Wheat (*Triticum aestivum* L.), is another crop species with high allelopathic potential, where naturally produced allelochemicals can be manipulated to eliminate weeds and ensure an environmentally friendly and sustainable agricultural production system. A variety of parameters affect wheat's biological potential, like that of all other allelopathic crops, such as its age, soil pH, carbon and nitrogen concentration, and soil water content. A variety of phytotoxic

compounds suspected of inducing allelopathic effects in wheat have been found and categorized into three major allelochemical categories: phenolic acids, hydroxamic acids, and fatty acids (Haig 2008). The presence of these secondary metabolites depends on plant family, species, and chemotype. The *Labiatae* family is notably rich in terpenoids and phenolic acids, the *Apiaceae* family coumarins and furanocoumarins, while hydroxamic acids and benzoxazinoids being abundant in the *Poaceae* family (Haig 2008).

Benzoxazinoids, including benzoxazinones and benzoxazolinones, are unique bioactive metabolites generated by some species of *Poaceae*, including wheat, that are allelopathic interference agents (Mwendwa et al. 2021). The most abundant of these acids in wheat is 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), which, together with 2,4-dihydroxy-2H-1,4-benzoxazin-3-one (DIBOA) and its associated microbial conversion products, are compounds with strong allelopathic effects on numerous broadleaf weeds (Latif et al. 2017). The highest amounts of benzoxazinoids are detected in young tissues of the roots and shoots, where they are glucosylated and stored in vacuoles or extruded by the roots. The soil is the primary medium through which allelochemicals, soil microorganisms, and their target plants interact, therefore its parameters such as organic matter, reactive mineral surfaces, ion exchange capacity, and inorganic ions have the main impact on allelochemical effects (Mwendwa et al. 2021).

Propionic acid, one of the fatty acids found in wheat residues, decreased the germination and development of annual ryegrass considerably. Allelopathic activity of *p*-coumaric acid and propionic acid in wheat accessions was associated with a decrease in germination in both resistant and susceptible annual ryegrass ecotypes. These effects have been reported in a variety of wheat tissues or organs, including shoots and roots; moreover, roots and their extracts have been proven to be more phytotoxic than other plant tissues (Hussain et al. 2022). Wheat also contains long-chained carboxylic acids such as oleic, linoleic, and stearic acids. These fatty acids decreased *Leptochloa chinensis* germination but did not affect the weed's root elongation (Haig 2008).

There are many reports that there is a strong genetic basis for conferring allelopathic potential in

wheat. Wu and co-workers reported that there are substantial genetic variations in allelopathic activity in wheat, thus providing a sufficient gene pool for the development of allelopathic wheat cultivars to suppress weeds (Wu et al. 2000). In their study, the authors showed that the normal distribution of allelopathic activity in the collection of 453 wheat accessions was similar to that reported in rice, indicating that wheat allelopathic activity is a quantitative trait (Wu et al. 2000).

6.3 Maize (*Zea mays* L.)

Zea mays is the third most cultivated food crop after rice and wheat. Apart from its consumption applications, it is an important resource to produce plastics, dyes, and packaging materials (Ahmed et al. 2022). It is now one of the driving models for plant utilitarian genomics and, because of its high phytochemical content, it is used to treat a variety of ailments (Ahmed et al. 2022). As early as 1983, it was shown that allelochemicals in maize are produced in all parts of the plant and are released into the environment because of root exudate seeping into the soil during rain leaching. Even maize pollen when it falls on plants growing nearby (such as bottle gourd, watermelon, etc.) causes a decrease in their fruiting (Mushtaq et al. 2020). The allelopathic potential of extracts from different plant parts of *Zea mays* was evaluated, and together with sorghum, it showed a pronounced inhibitory effect on germination and growth of wild barley (*Hordeum spontaneum*) (Al-Tawaha and Odat 2010). The compared allelopathic effects of several varieties of sunflower against problematic weed species in wheat were also evaluated (Alsaadawi et al. 2011). Scientists grew the allelopathic sunflower cultivars in a mixture with weeds or applied the residues of sunflower cultivars to the wheat crop and its weeds. It was observed that the sunflower varieties tested differed in their allelopathic effect and reduced total weed density by 10–87% and total weed biomass by 34–81%. The maize cultivars with a strong suppressive effect not only inhibited the growth of companion weeds but also reduced the population density and biomass of the weeds when their residues were introduced into the soil (Alsaadawi et al. 2011).

6.4 Rye (*Secale cereale* L.)

Another example of a crop with high allelopathic activity is rye, whose most important compounds responsible for this effect are benzoxazinones [2,4-dihydroxy-1,4(2H)-benzoxazin-3-one (DIBOA) and 2(3H)-benzoxazolinone (BOA)]. The researchers, after an extensive review of the allelopathic potential of rye, recorded 16 allelochemicals present in this plant, including β -phenyllactic acid, protocatechuic acid, DIBOA (glucoside), vanillic acid, apigenin-glycosides, syringic acid, luteolin-glucuronides, *p*-hydroxybenzoic acid, *p*-coumaric acid, benzoxazolinones BOA, cyanidin glycosides, β -hydroxybutric acid, isovitexinglucosides, DIMBOA (glucoside), gallic acid, and ferulic acid/conjugates (Schulz et al. 2013).

6.5 Sorghum (*Sorghum bicolor* L.)

Extensive literature explains also the allelopathic potential of sorghum and its implications in different cropping. Sorghum produces a variety of allelopathic compounds, the most important of which are hydrophobic *p*-benzoquinone (sorgoleone), phenolics, and acyanogenic glycoside (Abbas et al. 2021). Sorgoleone and its 1,4-dihydroxy form (resorcinol) represent 90% of the compounds present in sorghum root exudates (Głąb et al. 2017). A precise determination of the mechanism of sorghum root trichome formation can be used for the targeted use of sorghum as a mulch or cover crop for effective control of germinating weed seedlings. The action of sorgoleone can be compared to the action of the soil herbicide pendimethalin. A multidisciplinary approach to sorghum cultivation represents a promising prospective treatment using secondary metabolites that can also serve as lead compounds in herbicide discovery programs (Hussain et al. 2021).

6.6 Plant extracts as a source of allelochemicals

Another approach to weed control is using extracts from certain allelopathic plants, which reduce the occurrence of weeds by inhibiting germination and seedling growth. There are several papers in which the allelopathic potential of aqueous plant extracts under field conditions in the most significant crops such as wheat, maize, or cotton has been investigated,

presenting them with phytotoxic results expressed in terms of weed density and biomass reduction (Scavo and Mauromicale 2021). Examples from the literature are presented in Table 1, which was prepared based on articles Scavo and Mauromicale (2021), Cheema et al. (2013), Farooq et al. (2011). Among the most common aqueous plant extracts used for weed control are sorghum and sunflower, which in concentration at 12 L ha⁻¹ are efficient in limiting the dry weight of wild oats (*Avena fatua* L.) and canary grass (*Phalaris minor* Retz.), while at 6 L ha⁻¹ is the most economically viable treatment. The authors of these applications recommended applying the extract directly to the soil or growing media to mitigate phytotoxicity on the above-mentioned crops (Muhammad et al. 2009). Summarizing the chemical effects induced in plants by the treatment of these extracts, the authors highlighted that there was a significant increase in reactive oxygen species (ROS), suppression of the gibberellic pathway and accumulation of abscisic, salicylic and jasmonic acids, changes in cell membrane permeability and deregulation of nutrient uptake as well as modification of photosynthesis and respiration. Allelopathic plant extracts and synthetic herbicides can be used together to reduce the application doses of these harmful ones (Scavo and Mauromicale 2021). Selected examples of this combination are summarized in Table 2. An example of this approach is a study that used aqueous extracts of sorghum, sunflower, brassica (*Brassica campestris* L.), and mulberry (*Morus alba* L.) with a reduced dose of atrazine. It was concluded that a dose of atrazine alone and half of the dose of atrazine in combination with allelopathic plant aqueous extracts of sorghum, sunflower, brassica, and mulberry improved the reduction in weed density and dry biomass, thereby enhancing the grain yield and net income. Therefore, it may be concluded that the use of allelopathic plant extracts can effectively reduce herbicide usage rates for weed control (Khan et al. 2012). Encouraging results have been obtained in wheat, maize, cotton, and rice cultivation, but there are still not enough studies conducted to assess synergism between bioherbicides and synthetic herbicides. For more widespread application, it is crucial to understand the specific role of environmental factors on the bioavailability and effectiveness of allelochemicals. Environmental elements, mainly air and soil, act as carriers of allelochemicals, so pedoclimatic conditions can greatly influence the

Table 1 Effects of aqueous allelopathic plant extracts on weed suppression in field crops

Allelopathic cover crop	Dose (Extract concentration)	Crops benefited	Yield increase	Target weeds	Weed control (%)	References
Sunflower	0.1 L m ⁻² (10%)	Wheat	–	<i>Chenopodium album</i> L.	–70% of biomass	Anjum and Bajwa (2007)
Chinese cabbage	0.002 L m ⁻² (10%)	Mungbean	–	<i>Trianthema portulacastrum</i> L., <i>Cyperus rotundus</i> L	–14.6% of density and dry weight	Ullah et al. (2020)
Tree wormwood	4 L m ⁻² (18.82%)	Wheat	–52.9%	Several monocots and dicots, mainly <i>A. fatua</i> and <i>P. paradoxa</i>	~30% of weed suppression	Carrubba et al. (2020)
Sicilian sumac	4 L m ⁻² (8.75%)	Wheat	+9%		50.8% of weed suppression	
Common thyme	4 L m ⁻² (22.33%)	Wheat	–7.2%		~35% of weed suppression	
Common lantana	4 L m ⁻² (6.14%)	Wheat	+16.5%		16% of weed suppression	
Mediterranean spurge	4 L m ⁻² (2.27%)	Wheat	–2.3%		~40% of weed suppression	
Tree of heaven	0.001–0.002 g L ⁻¹ (20%)	Sage, rosemary, carnation	–	<i>Lepidium sativum</i> L., <i>Raphanus sativus</i> L.	0% weed presence in sage and rosemary, ~24% in carnation	Caser et al. (2020)
Sorghum	12 L ha ⁻¹	Cotton	+45.5%	<i>Trianthema portulacastrum</i> L.	Reduction in total weed density (47%) and dry weight (29%)	Cheema et al. (2002)
Sorghum	12 L ha ⁻¹	Wheat	+11%	<i>Fumaria indica</i> <i>Hauskn.</i> ,	Reduction in total weed density (21.6%) and dry weight (35.4%)	Cheema and Khaliq (2000)
Sorghum	12 L ha ⁻¹	Sunflower	+7.7%	<i>Cyperus rotundus</i> L.,	Reduction in total weed density (19.3%) and dry weight (27.2%)	Nawaz et al. (2001)
Sunflower + Rice + Brassica	4.5 t ha ⁻¹ each	Maize	41.0	<i>Trianthema portulacastrum</i>	60.1% weeds dry weight reduction	Khaliq et al. (2010)
Cotton + Sorghum	-	Maize	23.7	<i>Trianthema portulacastrum</i> , <i>Convolvulus arvensis</i>	92.0% weeds dry weight reduction	Iqbal et al. (2007)
Sorghum	0.0006 L m ⁻²	Wheat	+39%	<i>Avena fatua</i> L., <i>Phalaris minor</i> Retz.	21–41% weeds dry weight reduction 23–41% weeds dry weight reduction	Rehman et al. (2010)

Table 1 (continued)

Allelopathic cover crop	Dose (Extract concentration)	Crops benefited	Yield increase	Target weeds	Weed control (%)	References
Sorghum + sunflower	0.0006 L m ⁻² each	Wheat	+ 62%	<i>Avena fatua</i> L.,	24–39% weeds dry weight reduction	Muhammad et al. (2009)
				<i>Phalaris minor</i> Retz.	30–35% weeds dry weight reduction	
Sorghum + sunflower	0.00012 L m ⁻² each	Wheat	+ 53.5%	<i>Avena fatua</i> L.,	42–62% weeds dry weight reduction	
				<i>Phalaris minor</i> Retz.	36–55% weeds dry weight reduction	
Sorghum + eucalyptus	0.0006 L m ⁻² each	Wheat	+ 47.5%	<i>Avena fatua</i> L.,	28–3% weeds dry weight reduction	
				<i>Phalaris minor</i> Retz.	13–28% weeds dry weight reduction	
Sorghum + sesame	0.00006 L m ⁻² each	Wheat	+ 44%	<i>Avena fatua</i> L.,	21–24% weeds dry weight reduction	
				<i>Phalaris minor</i> Retz.	19–24% weeds dry weight reduction	
Sorghum + tobacco	0.0006 L m ⁻² each	Wheat	+ 18.5%	<i>Avena fatua</i> L.,	14% weeds dry weight reduction	
				<i>Phalaris minor</i> Retz.	10–14% weeds dry weight reduction	
Sorghum + brassica	0.00006 L m ⁻² each	Wheat	+ 19%	<i>Avena fatua</i> L.,	18–24% weeds dry weight reduction	
				<i>Phalaris minor</i> Retz.	21–27% weeds dry weight reduction	

transport and retention of these compounds (Scavo and Mauromicale 2021). Regarding weed management in wheat crops, it was proven that the dose of isoproturon could be reduced by as much as 60% following the application of a mixture of an aqueous extract of sorghum (Farooq et al. 2011). It was also discovered that the combination of an aqueous extract of sorghum and pedimentalin at a dose equivalent to one-third of the standard amount resulted in a higher

cotton yield than the application of the full dose of synthetic herbicide, even though weed suppression was relatively lower. Reduced doses of pedimentalin were also combined with aqueous extracts from sorghum, sunflower, brassica, and rice demonstrating that 50–67% less herbicide in combination with allelopathic aqueous extracts can be effective in controlling weeds and increasing oilseed canola yields (Farooq et al. 2011).

Table 2 Weed control through a combination of allelopathic aqueous extracts with a reduced dose of herbicides

Crop	Allelopathic extract (Rate)	Herbicide (Rate)	Weed species	Weed control [%]		References		
				Standard dose herbicide	Herbicide (1/2 dose) + allelopathic extract			
Rice (<i>Oryza sativa</i> L.)	Sorghum + Sunflower + Rice (15 L ha ⁻¹ each)	Butachlor (1200 g a.i. ³ . ha ⁻¹)	<i>Echinochloa crusgalli</i>	WD ^b 80%	WD 80%	Rehman et al. (2010)		
				DW ^c 79%	DW 66%			
			<i>Cyperus iria</i>	WD 79%	WD 67%			
			DW 74%	DW 71%				
		<i>Dactyloctenium aegyptium</i>	WD 76%	WD 74%				
			DW 80%	DW 76%				
		Sorghum + Sunflower + Rice (15 L ha ⁻¹ each)	Pretilachlor (625 g a.i. ha ⁻¹)	<i>Echinochloa crusgalli</i>	WD 82%		WD 76%	
					DW 73%		DW 60%	
				<i>Cyperus iria</i>	WD 83%		WD 66%	
		DW 75%	DW 60%					
	<i>Dactyloctenium aegyptium</i>	WD 82%	WD 74%					
		DW 85%	DW 81%					
	Sorghum + Sunflower + Rice (15 L ha ⁻¹ each)	Ethoxysulfuronethyl (30 g a.i. ha ⁻¹)	<i>Echinochloa crusgalli</i>	WD 81%	WD 72%			
				DW 73%	DW 62%			
			<i>Cyperus iria</i>	WD 79%	WD 69%			
			DW 75%	DW 64%				
<i>Dactyloctenium aegyptium</i>			WD 85%	WD 75%				
			DW 82%	DW 69%				
Sorghum (15 L ha ⁻¹ each)	Penaxolam (30 mL a.i. ha ⁻¹)	<i>Echinochloa crusgalli</i>	DW 26%	DW 35%	Wazir et al. (2011)			
		<i>Echinochloa colonum</i>						
		<i>Cyperus rotundus</i>						
		<i>Cyperus iria</i>						
		<i>Dactyloctenium aegyptium</i>						
Wheat (<i>Triticum aestivum</i> L.)	Sorghum (12 L ha ⁻¹ each)	Isoproturon (1 kg a.i. ha ⁻¹)	<i>Phalaris minor</i>	WD 94%	WD 94%	Cheema et al. (2003)		
				DW 79%	DW 65%			
			<i>Melilotus parviflora</i>					
			<i>Coronopus didymus</i>					
	Sorghum + Sunflower (18 L ha ⁻¹ each)	Bensulfuron + Iso-proturon (1,050 g a.i. ha ⁻¹)	<i>Phalaris minor</i>		WD 85%	WD 89%	Razzaq et al. (2010)	
					DW 93%	DW 95%		
			<i>Coronopus didymus</i>		WD 82%	WD 88%		
					DW 64%	DW 87%		
			Metribuzin (175 g a.i. ha ⁻¹)	<i>Phalaris minor</i>		WD 92%		WD 69%
						DW 46%		DW 83%
		<i>Coronopus didymus</i>		WD 91%	WD 88%			
				DW 77%	DW 98%			
		Metribuzin + phenoxaprop (190 g a.i. ha ⁻¹)	<i>Phalaris minor</i>		WD 89%	WD 83%		
					DW 92%	DW 97%		
				<i>Coronopus didymus</i>	WD 87%	WD 87%		
			DW 91%	DW 94%				
Mesosulfuron + idosulfuron (120 g a.i. ha ⁻¹)	<i>Phalaris minor</i>		WD 42%	WD 89%				
			DW 85%	DW 98%				
		<i>Coronopus didymus</i>	WD 91%	WD 87%				
		DW 74%	DW 93%					

Table 2 (continued)

Crop	Allelopathic extract (Rate)	Herbicide (Rate)	Weed species	Weed control [%]		References
				Standard dose herbicide	Herbicide (1/2 dose) + allelopathic extract	
Maize (<i>Zea mays</i> L.)	Sorghum + Brassica + Sunflower + Mulberry (20 L ha ⁻¹ each)	Atrazine (500 g a.i. ha ⁻¹)	<i>Trianthema portulacastrum</i> L	WD 38% DW 94%	WD 36% DW 90%	Khan et al. (2012)
			<i>Convolvulus arvensis</i> L	DW 64%	DW 57%	
Sunflower (<i>Helianthus annuus</i> L.)	Sorghum + Sunflower (15 L ha ⁻¹ each)	Pendimethalin (825 mL a.i. ha ⁻¹)	<i>Chenopodium album</i> <i>Melilotus indica</i>	WD 95% DW 86%	WD 84% DW 67%	Awan et al. (2009)
			<i>Amaranthus retroflexus</i>			
Canola (<i>Brassica napus</i> L.)	Sorghum + Brassica (15 L ha ⁻¹ each)	Pendimethalin (1.2 kg a.i. ha ⁻¹)	<i>Trianthema portulacastrum</i>	WD 100% DW 100%	WD 91% DW 94%	Jabran et al. (2008)
			<i>Cyperus rotundus</i>	WD 32% DW 6%	WD 43% DW 38%	
			<i>Chenopodium album</i>	WD 78% DW 83%	WD 74% DW 62%	
			<i>Coronopus didymus</i> L	WD 39% DW 37%	WD 66% DW 71%	

^aa.i.—active ingredient

^bD—weed density

^cDW—dry weight

7 Biotechnology tools for understanding allelopathic interactions

Many studies have pointed out the high dependence of allelopathic potential on genotype, as there are differences between varieties in allelochemical concentrations and allelopathic activity. Rice, wheat, rye, barley, and sorghum are the most researched allelopathic crops, with considerable allelochemical differences depending on the cultivar (Scavo and Mauromicale 2021). A novel approach to plant cultivation uses the biotechnological transfer of allelopathic traits between cultivars of the same species or between species. This concept is based on selective and efficient screening of the occurrence of allelopathic characteristics using several molecular markers (Amb and Ahluwalia 2016).

Modern techniques make it easier to locate genes conferring allelopathic traits. These genes can be cloned and incorporated into current commercial varieties and other plants with competitive components (e.g., early vigor, wide leaf area, fast seedling emergence, root development, plant height,

and tillering). This approach would be a milestone toward the further development of sustainable crop production systems with less dependence on herbicides (Wu et al. 2002). Conventional breeding methods are more easily introduced for plant breeders because of the public concerns arising from transgenic crops (Wu et al. 2002). It is essential to ensure that genetic modifications with allelochemicals do not damage the environment, humans, animals, and other non-target organisms, as well as monitor for potential effects on different varieties or weed species (Wu et al. 2002).

However, polygenicity and the low economic added value make breeding methods very difficult (Scavo and Mauromicale 2021). Allelopathy is a polygenetic trait poorly connected to yield, necessitating the modification of several genes to encode the synthesis of allelochemicals. This has been found in the case of benzoxazinoids such as DIMBOA and DIBOA in *Poaceae* members, for example (Scavo and Mauromicale 2021). The allelochemicals' fate is mainly determined by the developmental stages of the plant and the conditions of the external environment.

Genetic modification can modulate the production and release of allelochemicals, and the potential for crop weed control can be improved (Wu et al. 2002).

However, the challenge for scientists is to determine the mechanism of inheritance of allelopathic agents and to isolate and quantify the compounds responsible for these properties. A certain complication is a case when more than one gene encoding special enzymes is required to increase the synthesis of a given allelochemical. This situation occurred in the case of the DIMBOA compound synthesized by different grass species. In maize, for example, the biosynthesis of this compound is determined by five genes encoding three enzymes (Soltys et al. 2013). The genes involved in synthesizing allelochemicals and genetic engineering tools, such as recombinant DNA, polymerase chain reaction, and metabolic engineering, have been developed to understand metabolic pathways better (Scavo and Mauromicale 2021).

Analysis of quantitative trait loci (QTLs) based on amplified fragment length polymorphism (AFLP) and restriction fragment length polymorphism (RFLP) is used to identify genetic markers responsible for conferring allelopathic traits (Scavo and Mauromicale 2021). These markers are used by scientists to systematically map and distinguish genes crucial in conferring quantitative traits (Wu et al. 2002). Through marker-assisted selection in crop breeding programs, linkage analysis of genetic markers and QTLs may increase genetic gains for allelopathic activity (Wu et al. 2002). Given the potential benefits of allelopathy for the cultivation of commonly produced crop plants such as rice, wheat, and sorghum, various researchers have proposed improving crop cultivar allelopathic qualities by traditional breeding or genetic modification (Mohammadi 2013).

Rice diterpenoid momilactones are natural compounds with correlative biochemical evidence suggesting a function in allelopathy. Researchers apply reverse genetics and knock-outs of the appropriate diterpene synthases to prove that rice momilactones are involved in allelopathy, such as reducing the development of the typical rice paddy weed, barnyard grass (*Echinochloa crus-galli*). The inducible nature of momilactone formation in rice implies that similar induction may enhance rice's endogenous ability to control weed development (Xu et al. 2012). Another example is in screening for the alkaloids gramine, hordenine, and its direct precursor *N*-methyltyramine

in barley (Scavo and Mauromicale 2021). The researchers discovered a significant difference based on plant parts between wild relatives and modern genotypes, thus providing essential advance in breeding this plant (Scavo and Mauromicale 2021).

8 Allelopathic practices used for weed control

Allelopathic interaction plays an important role in agricultural ecosystems due to its influence on crop plant development. Several variables need to be taken into consideration when using allelopathy for weed control, such as the weed species, climatic conditions, type of agricultural practices, and economic aspects. The phenomenon of allelopathy may provide a new front in integrated weed control by including them in rotational sequences or intercropping near a cash crop, cover cropping as living or dead mulches, and crop residue incorporation into the soil (Scavo and Mauromicale 2021). There is a feasible perspective of using the allelopathic mechanism as an environmentally friendly tool for weed control in cropping systems without dependence on chemical herbicides. The incorporation of allelopathic plants into agricultural strategies will improve sustainable crop production due to the positive effects of these practices on soil fertility, organic matter content, and ecosystem biodiversity (Abbas et al. 2021).

Intercropping is the simultaneous cultivation of different crops at the same time in the same field, especially using allelopathic species, which have a high potential to control weeds in an environmentally friendly approach. The selective combination of yield-improving crops promotes farm diversification and provides economic benefits (Khamare et al. 2022). This type of cultivation is a great way to make efficient use of natural resources, increase biodiversity, control pests, and improve crop yield and quality, as well as natural soil fertility while using fewer off-farm inputs (Glaze-Corcoran et al. 2020). Evaluating the effectiveness of intercropping main crops with allelopathic plants, there is general agreement on the potential for weed control through the release of allelochemicals (Abbas et al. 2021). In a certain field trial, the intercropping of legumes with wheat was evaluated for weed suppression compared with the sole wheat crop (Abbas et al. 2021). The intercrops in the experiment included white clover (*Trifolium repens*

L.), black medic (*Medicago lupulina* L.), alfalfa, and red clover (*Trifolium pratense* L.). The intercrops reduced weed density in the following crop, and red clover was the most effective intercrop for suppressing weeds in organically grown wheat. In a similar study, intercultivation of pea (*Pisum sativum* L.) with barley (*Hordeum vulgare* L.) sorghum with pea (*Vigna unguiculata* (L.) Walp.) wheat with rape and wheat with chickpea (*Cicer arietinum* L.) was used (Abbas et al. 2021). In all instances, intercropping allelopathic plants with the main crop can reduce weed intensity and improve yield gains. Properly carried out intercropping is efficient in terms of the use of natural resources and increases biodiversity as well as crop quality.

Crop rotation is a cultivation strategy in which different crops are grown in a specific order. A well-designed crop rotation ensures the formation of an unstable environment for weeds. Crop rotations change growth conditions from year to year, creating a situation in which only a few weeds are readily adaptable. Continuous monoculture exacerbates weed and pathogen pressure and difficulties in maintaining soil fertility. Crop rotations can be used by rotating early, late and autumn crops; grasses, broadleaves, and legumes; highly competitive crops with less competitive crops; annual and perennial crops; alternating between closed, dense crops which shade out weeds and open crops (Mamolos 2008). In this cultivation method, allelopathic plants use allelochemicals secreted by the roots and released by the decomposition of residues from previous crops to suppress weeds. These released allelocompounds also help to improve soil organic matter and microorganisms and increase soil fertility and yields (Scavo and Mauromicale 2021). An example of this is sunflower-wheat rotation, which effectively reduced weed infestation in the wheat crop after sunflower, as well as the wheat crop after sorghum. The literature proved that including canola in the rotation resulted in an approximately 40% reduction in weed density in the next crop in the rotation (Abbas et al. 2021). A scheme of selected agricultural practices using allelopathic potential is presented in Fig. 6.

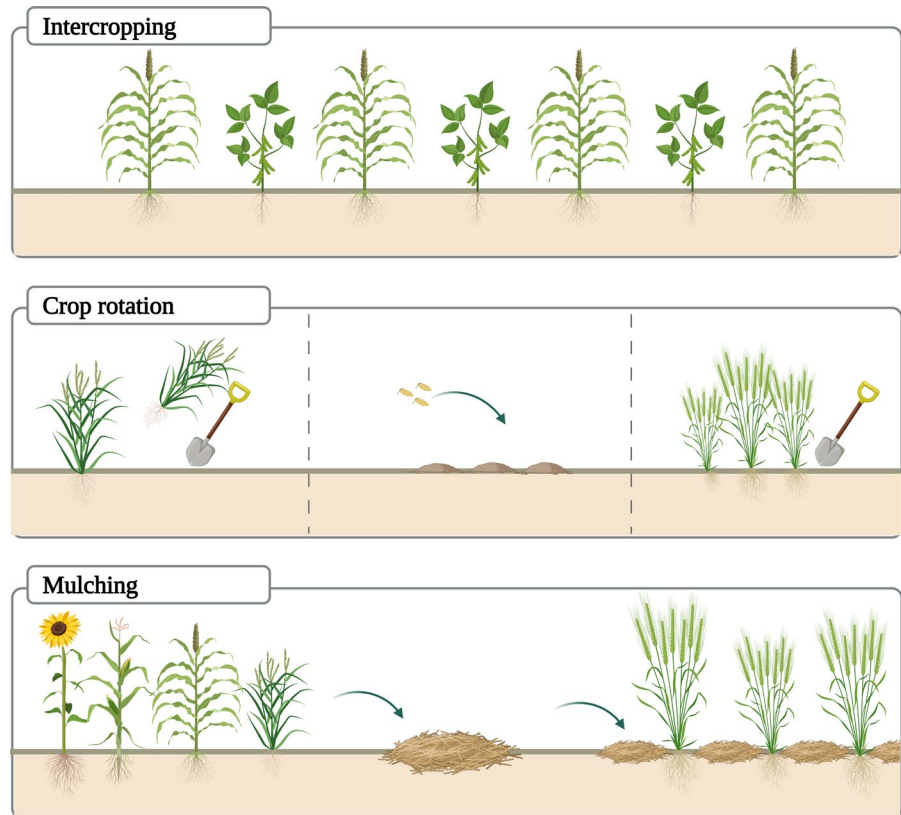
In allelopathic mulching, the crop or weed residues are spread over the soil surface or incorporated into the soil to suppress weeds (Abbas et al. 2021). Several studies have proven that mulches with the allelopathic crop can be a preventive weed control by

affecting the soil weed seedbank, weed emergence, and establishment (Scavo and Mauromicale 2021). Additional benefits of using allelopathic plant residues for sustainable agriculture include increased soil fertility, increased soil organic matter, improved water infiltration into the soil, regulating soil temperature, and reduced soil erosion (Farooq et al. 2011). Farmers generally use the economic parts of the crop and incorporate the remaining parts of the crop into the field as organic matter (Abbas et al. 2021). A study showed that the use of sorghum straw as a mulch in maize enabled 37% weed control, while in rice and cotton, the use of sorghum mulch provided as much as 50% and 60% weed control, respectively (Abbas et al. 2021). The residues of various crops such as rye, clover, rice, maize, and canola have been reported for their potential as weed control (Abbas et al. 2021). The application of mulches of allelopathic crops including rice, maize, sorghum, and sunflower at 12 t ha⁻¹ provided effective control of herbicide-resistant *Phalaris minor* in wheat. The combination of different allelopathic plant residues increases weed control potential due to the synergistic effects of allelochemicals. Another example of this approach could be the combined use of canola, sunflower, and sorghum mulches which provided more efficient weed control in maize as compared to the sole use of individual mulch material (Scavo and Mauromicale 2021).

9 Allelochemicals as bioherbicides

Changing consumer preferences and demand for organically produced food make bioherbicides suitable alternatives to man-made herbicides. Intending to reduce the use of synthetic herbicides, overcome weed-resistance phenomena and minimize their environmental impact, plant-based allelochemical bioherbicides are gaining in popularity (Scavo and Mauromicale 2021). Natural products degrade quickly, making them much safer to use in the environment (Lengai and Muthomi 2018). Most allelopathic compounds are totally or partially water-soluble which makes them easier to apply without additional surfactants. Allelochemicals have an environmentally friendly chemical structure compared to synthetic equivalents (Scavo and Mauromicale 2021). They possess higher oxygen-, nitrogen, and sp³-hybridized carbon molecules with relatively few so-called

Fig. 6 Scheme of practical applications of allelopathic cover cropping by intercropping, crop rotation, and mulching crop residues (created with <https://www.biorender.com/>)



'heavy atoms', a halogen substitute, and are characterized by the absence of 'unnatural' rings. These features reduce a compound's environmental half-life, preventing accumulation in soil and interference with non-target plants and organisms (Soltys et al. 2013).

The development of bioherbicides is much more complicated in contrast to synthetic ones because bioactive substances must first be properly isolated from plant extracts and the extractable mass of compounds recovered is usually small compared to the simple process of producing large quantities of synthetic herbicides by chemical synthesis (Soltys et al. 2013). Before an allelochemical can be used as an herbicide, it must meet certain criteria. It is necessary to identify its chemical structure, know its mechanism of action in plants, determine its residence time in the soil, its effect on the environment and non-target plants, its possible toxicity to human health as well as toxicity to terrestrial and aquatic lifeforms, as well as the profitability of production on a commercial scale (Soltys et al. 2013). The general steps of bioherbicide development are shown in Fig. 7.

Allelopathic compounds could be used as templates to synthesize novel herbicides. For example, several studies have been performed to develop new herbicides using coumarins because of their bioactivity, and the results showed that some of the novel compounds had the same inhibitory effect on weeds as the commercial herbicide acetochlor (Zhao et al. 2021). In their latest study, Zhao et al. (2021), designed and synthesized a series of new phenoxy pyridine derivatives containing the natural product coumarin. These compounds showed excellent herbicidal activity under greenhouse conditions, similar to the commercial herbicide oxyfluorfen. The herbicidal activity of these compounds was significantly affected by the types of substituents introduced at the phenoxy pyridine and coumarin rings. The introduction of an electron-withdrawing group on the first one increased the extent of activity. The visual injury and growth status of the test crops were observed at regular intervals and the crop selectivity tests showed that maize, cotton, and soybean had excellent tolerance to the new compound, but rice and wheat were damaged (Zhao

et al. 2021). In a recent study, some researchers examined how the addition of organic amendments and organo-clays altered the sorption and persistence of scopoletin in soil. Galán-Pérez et al. (2022) showed that sorption and microbial activity changes both appeared to contribute to increasing the persistence of the allelochemical in amended soil. This study has shed more light on the application of allelochemical-based herbicides by modifying appropriate soil additives, to effectively use the bioactivity of allelochemicals for organic weed control in a simple way (Galán-Pérez et al. 2022).

Bioherbicides are prepared from parts of plants obtained from the environment or man-made—fully synthetic, or created on the model of natural substances, which are cleaned of dirt or foreign materials. The plant-based material prepared in this way is then extracted using solvents or distilled to obtain respective extracts or essential oils (Lengai and Muthomi 2018). The quality of the extracts obtained is influenced by the type of solvent used and the extraction method. Dried plant parts are generally preferred due to higher yields of the active ingredient. Solvents with low toxicity, high capacity to dissolve large amounts of compounds, easy evaporation, and preservative properties should be used for extraction.

Organic solvents such as ethanol and methanol are the most effective, compared to water which, although a very versatile solvent, extracts significantly fewer compounds (Lengai and Muthomi 2018).

Bioherbicides are formulated based on weed control's most active botanical ingredients under field conditions (Kremer 2019). These ingredients are identified and evaluated for optimal formulation. Bioherbicide formulations consist of an active ingredient, a carrier, and excipients that create protection during exposure to adverse environmental conditions and support optimal weed control performance (Kremer 2019). Stabilizers and carriers aim to increase the durability and stability of the compound, whereas formulation-type components ease handling and increase efficiency and applicability. They also facilitate its non-degradability when exposed to environmental factors. The challenge of the widespread use of bioherbicides is to optimize formulation and application methods that will allow the active agent to be evenly introduced to the targeted area without excessive use of the product. Precise application of the substance at the site of the weed to be controlled without exposing the crop significantly increases the effectiveness of the bioherbicide (Kremer 2019). After many laboratory and field trials using various combinations of

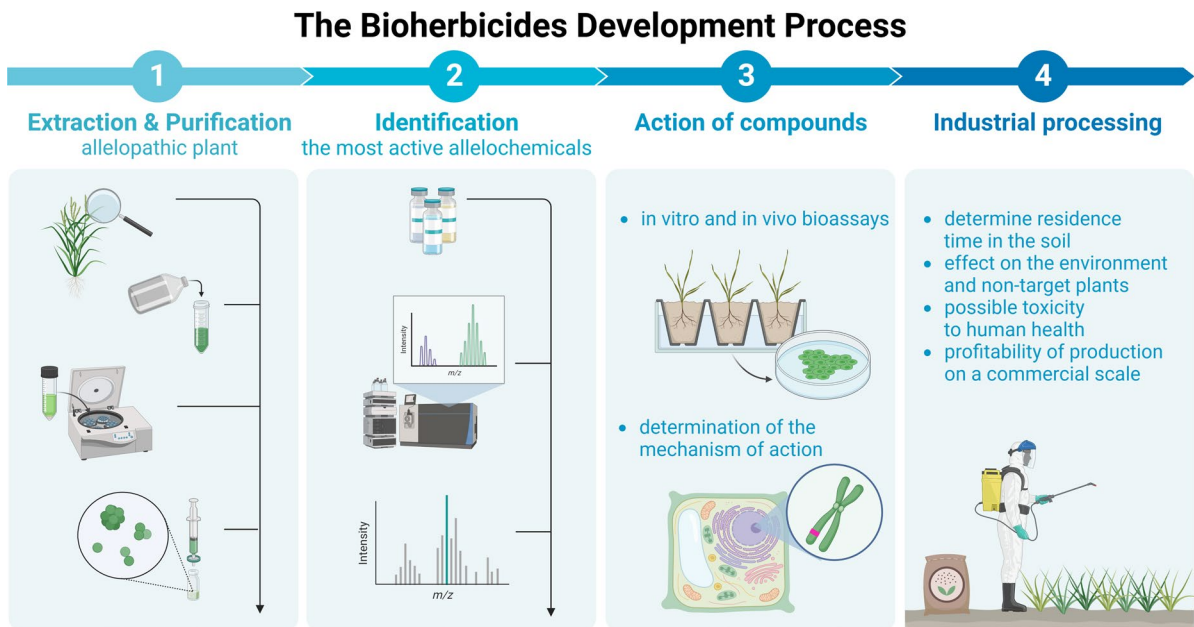


Fig. 7 Steps for producing commercial bioherbicides (created with <https://www.biorender.com/>)

active ingredients and additives, reports are created as the basis for submitting a product registration application to the applicable state authorities (Lengai and Muthomi 2018).

One should bear in mind that the cost of bioherbicides must be competitive to become realistic alternatives to conventional herbicides. Thus, new plant protection methods should be developed in a way that minimizes the cost of crop production (Głąb et al. 2017). Given the above-stated reasons, the imperative is finding an optimal solution that would simplify the procedures and enable the development of new bioherbicides with a competitive price acceptable to agricultural producers and thus increase their application (Šunjka and Mechora 2022).

However, the widely developed bioinformatics and cheminformatics overcome these challenges by supporting the discovery of new bioherbicides compounds (Soltys et al. 2013). The precisely identified and characterized chemical structure of allelochemicals is the basis for designing products with analogous properties using specialized computer programs. Chemoinformatic tools can propose structures of similar compounds and, after several alterations, lead to improvements in their activity and stability. An example of this was the modification of leptospermone (Soltys et al. 2013). Owing to its herbicidal properties leptospermone—a triketone identified in 1977—has been used to create numerous highly active chemical analogs such as Sulcotrione[®] and Mesotrione[®]. Other products that are not herbicides per se, but have been synthesized and produced based on natural molecules are phosphinothricin (a biosynthetic version of glufosinate) and bialophos (a microbial phytotoxic product) (Cordeau et al. 2016).

While bioherbicides provide such advantages as a safe environment and healthy food for human consumption, some factors limit their full adoption in weed control. The biodegradation, type, and concentration of allelochemicals released into the environment depend on the combined effects of the plant itself and environmental factors which are sometimes difficult to control (Scavo and Mauromicale 2021). The relatively short environmental half-life of allelochemical substances is good from an environmental toxicology standpoint. However, a herbicide must persist sufficiently long to have the desired effect and to be effective (Motmainna et al. 2021). The design of new bioherbicides also needs to be mindful that

allelopathic effects vary between varieties or genotypes because it is not necessarily that plants with close taxonomic proximity have similar allelopathic effects (Motmainna et al. 2021). It is also worth remembering that, compared to synthetic herbicide, the botanical herbicide releases into the environment mixture of allelochemicals, with a qualitative and quantitative composition that is difficult to precisely predict. A single allelopathic compound may not show allelopathic activity individually in a certain situation but might increase allelopathy in association with other allelochemicals. It is therefore important to evaluate interactions such as synergy, antagonism, and incremental effects, between different allelochemicals (Motmainna et al. 2021). Allelochemicals have multi-site action in plants without the high specificity which is achieved in the case of synthetic herbicides and are also highly dose-dependent. Under field conditions, high doses of allelochemicals are necessary to achieve the desired efficacy, and the concentration of these bioactive components is dictated by the environment under which they grow (Scavo and Mauromicale 2021).

10 Conclusions

Although there are an increasing numbers of reports on the use of allelopathy under field conditions, unfortunately, most studies do not attempt to understand the modes of action that drive these interactions and there is a lack of knowledge on the ecotoxicological impact of bioherbicides. This knowledge would optimize the conditions for the use of allelochemicals and encourage their use as bioherbicides. Allelochemicals should not be excluded despite many limitations, as they can contribute to towards improvement of crop productivity and environmental protection through eco-friendly control of weeds, crop diseases, and conservation of nitrogen in croplands.

The use of chemoinformatic methods to identify the chemical structures and mechanisms of action of allelochemicals can be a starting point for designing formulations with compound-like properties and the synthesis of novel agrochemicals based on natural products. Further research and regulation are needed to increase the number of effective solutions in the global bioherbicide market (Soltys et al. 2013). Therefore, a holistic approach to this

remarkable phenomenon is proposed to design experiments appropriate to the species and ecosystems under investigation, using multidisciplinary programs to implement allelopathy as a useful tool for weed control.

Acknowledgements No funding was received to assist with the preparation of this manuscript.

Author contributions MK-B designed the conception of the review, conducted the literature research, and wrote the manuscript. JP read the first draft of the article. HB critically revised the manuscript. All authors read and approved the final version of the manuscript.

Declarations

Competing interests All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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