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Allelopathy and sustainable weed management in the era of herbicide resistance and regulatory restrictions

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SUMMARY

For decades, chemical weed control has played a crucial role in agriculture by controlling weeds and ensuring sustainable crop productivity. Years of relying on herbicides with the same mode of action have accelerated the development of resistant weed biotypes. Today, this agronomic challenge is further complicated by strict European Union regulations, which restrict chemical control options through the gradual phase-out of key active ingredients. The use of non-chemical weed control methods within the framework of Integrated Weed Management (IWM) is now essential for long-term sustainable food production. In this context, allelopathy represents a sustainable ecological approach that utilizes plants and their bioactive allelochemicals to suppress weed interference. This review evaluates agroecological alternatives to herbicide dependence, focusing on the application of allelopathic aqueous extracts and essential oils, while specifically highlighting the potential of allelochemicals as natural herbicides. Embedding allelopathy within IWM frameworks shifts the focus from conventional chemical control toward novel strategies. By introducing alternative biological suppression pathways through allelopathic crop management, this agroecological approach effectively diversifies selection pressures and stalls resistance development. The successful integration of these strategies within modern agriculture can substantially mitigate herbicide dependency and enhance ecosystem stability.

Keywords: herbicide resistance, European Union regulations, allelopathy, natural herbicides, Integrated Weed Management.

INTRODUCTION

Globally, weed infestation represents one of the most persistent biotic constraints to agricultural production. Weeds compete directly with crops for essential resources such as light, nutrients, moisture, and space, thereby severely restricting crop development and final yields (Khamare et al., 2022). To ensure yield stability, modern agricultural systems have historically relied on synthetic herbicides as their primary tool for weed suppression. However, this intensive chemical reliance has triggered the rapid evolution of herbicide resistance. This evolutionary phenomenon spans all major herbicide sites of action, including acetolactate synthase (ALS), photosystem II (PSII), acetyl-CoA carboxylase (ACCase), and 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) inhibitors, as well as synthetic auxins (Heap, 2026). Among these, ALS inhibitors account for the highest incidence of resistant cases due to their overuse in intensive cropping systems (Hulme, 2022; Riechers et al., 2024; Heap, 2026). Parallel to the agronomic challenges of herbicide resistance, growing public concerns regarding the environmental and human health impacts of intensive chemical inputs have fundamentally reshaped statutory frameworks. The widespread application of synthetic herbicides is increasingly linked to non-target toxicity, biodiversity loss, and contamination of soil and groundwater ecosystems (Tang et al., 2021; Bacmaga et al., 2024). In response to these cumulative ecotoxicological risks, regulatory frameworks, most notably within the European Union under Regulation (EC) No 1107/2009 and the Farm to Fork Strategy, have shifted weed control toward stringent, hazard-based precautionary principles (Kudsk and Mathiassen, 2020; Möhring et al., 2020). This legislative shift has led to the non-renewal and rapid withdrawal of numerous critical active ingredients, systematically reducing the number of effective chemical control options available to agrosystems (European Commission, 2020). The convergence of accelerating herbicide resistance, a multi-decadal stagnation in novel mode of action (MoA) discovery, and tightening regulatory restrictions underscores an urgent necessity for a transition toward agroecological approaches which would secure long-term weed suppression (MacLaren et al., 2020; Scavo and Mauromicale, 2021; Gerhards et al., 2024). Within the framework of Integrated Weed Management (IWM), utilizing plant-derived allelochemicals as natural growth inhibitors offers a viable, bio-based strategy for reducing synthetic reliance (Duke et al., 2000; Khamare et al., 2022; Kostina-Bednarz et al., 2023). These novel suppression pathways diversify selection pressures within weed management systems, thereby stalling resistance development (Khamare et al., 2022; Kostina-Bednarz et al., 2023). The focus of this review is to synthesize current knowledge on allelopathy's role and positioning, and examine how it may be integrated into IWM frameworks in the era of escalating herbicide resistance and regulatory restrictions. Additionally, the physiological mechanisms underlying these biochemical interactions are analyzed, the phytotoxic potential of aqueous extracts and essential oils as natural herbicides is evaluated, and the technological advancements and future research prospects required to translate laboratory efficacy into reliable field-scale agronomic practice are discussed.

CURRENT CHALLENGES IN HERBICIDE-BASED WEED MANAGEMENT

Herbicides have become an indispensable component of modern agricultural systems due to their efficiency in controlling weeds and supporting high crop productivity. Nonetheless, their extensive and often repetitive use has led to a range of agronomic, environmental, and regulatory challenges. In recent decades, increasing concerns regarding herbicide resistance, environmental contamination, human health risks, and tightening regulatory frameworks, particularly within the European Union, have significantly reshaped the discourse on herbicide sustainability. These challenges call for a transition toward more integrated and ecologically based weed management strategies.

Global trends and mechanisms of herbicide resistance. One of the most critical constraints in modern weed management is the rapid evolution of herbicide-resistant weed populations. Herbicide resistance is defined as the inherited ability of a plant to survive and reproduce following exposure to an herbicide dose that would normally be lethal to susceptible biotypes (Powles and Yu, 2010). The evolution of resistance is primarily driven by repeated use of herbicides sharing the same MoA over multiple seasons, which imposes strong and continuous selection pressure on weed populations. Under such conditions, naturally occurring resistant individuals are selectively favored, leading to progressive shifts in population structure and eventual control failure (Duke, 2012; Heap, 2014).

The first confirmed case of herbicide resistance was reported in the late 1950s in *Senecio vulgaris* selected by triazine herbicides (Ryan, 1970). Since then, herbicide resistance has expanded exponentially across agroecosystems worldwide. According to the latest global data, more than 540 weed species have evolved resistance to at least one herbicide mode of action across over 100 countries and numerous cropping systems (Table 1). Resistance has been documented for all major herbicide MoA, including acetolactate synthase inhibitors, photosystem II inhibitors, acetyl-CoA carboxylase inhibitors, EPSPS inhibitors (glyphosate), and synthetic auxins. Among these, ALS inhibitors account for the highest number of resistant cases globally, followed by PSII and EPSPS inhibitors, reflecting their historical overuse and widespread adoption in intensive cropping systems (Heap, 2026; Figure 1).

Table 1. Herbicide-resistant weeds by site of action.

HRAC group	Legacy HRAC group	Site of action	Example herbicides	Dicots	Mono-cots	Total
2	B	Inhibition of acetolactate synthase	Chlorsulfuron	108	68	176
5	C1 C2	PSII inhibitors - serine 264 binders	Chlorotoluron	53	36	89
9	G	Inhibition of enolpyruvyl shikimate phosphate synthase	Glyphosate	29	33	62
1	A	Inhibition of acetyl-CoA carboxylase	Sethoxydim	0	55	55
4	O	Auxin mimics	2,4-D	35	9	44
22	D	PS I electron diversion	Paraquat	23	10	33
14	E	Inhibition of protoporphyrinogen oxidase	Oxyfluorfen	13	5	18
3	K1	Inhibition of microtubule assembly	Trifluralin	2	10	12

15	K3 N	Very long-chain fatty acid synthesis inhibitors	Butachlor	2	8	10
27	F2	Inhibition of hydroxyphenyl pyruvate dioxygenase	Isoxaflutole	4	3	7
10	H	Inhibition of glutamine synthetase	Glufosinate-ammonium	2	5	7
34	F3	Inhibition of lycopene cyclase	Amitrole	1	5	6
6	C3	PSII inhibitors - histidine 215 binders	Bromoxynil	3	2	5
12	F1	Phytoene desaturase inhibitors	Diflufenican	4	1	5
29	L	Inhibition of cellulose synthesis	Dichlobenil	0	4	4
0	Z	Unknown	Endothall	0	4	4
13	F4	Inhibition of deoxy-D-xylulose phosphate synthase	Clomazone	0	3	3
0	Z	Antimicrotubule mitotic disrupter	Flamprop-methyl	0	3	3
23	K2	Inhibition of microtubule organization	Propham	0	1	1
0	Z	Nucleic acid inhibitors	MSMA	1	0	1
0	Z	Cell elongation inhibitors	Difenzoquat	0	1	1
				280	266	546

Herbicide resistance is classified into two primary categories: target-site resistance

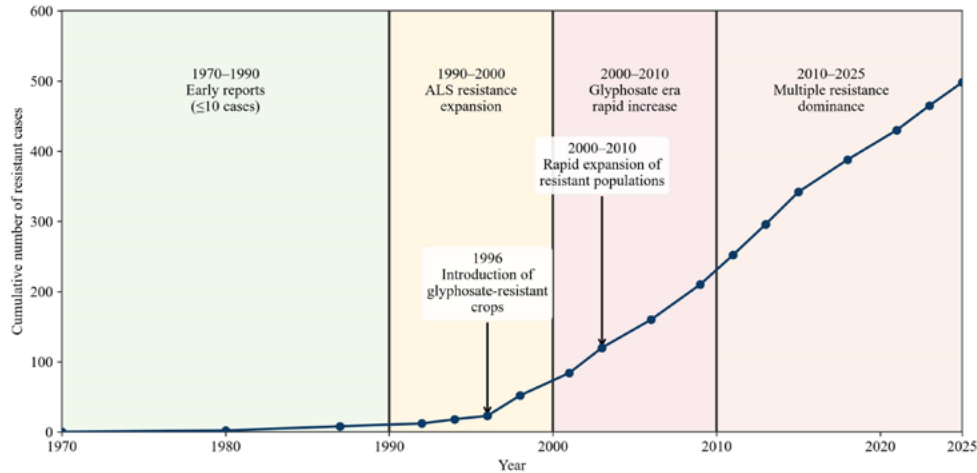


Figure 1. Chronological evolution of global weed resistance (1970-2025).

(TSR) and non-target-site resistance (NTSR). While TSR typically stems from gene amplification or point mutations that disrupt herbicide binding, NTSR involves more complex cellular mechanisms such as enhanced metabolic detoxification, reduced translocation, and sequestration, often mediated by cytochrome P450 monooxygenases, glutathione S-transferases, and other detoxification systems (Gaines et al., 2020; Hulme, 2022). Recent data shows that NTSR is now rising globally. Because it can confer cross-resistance across entirely different herbicide MoA, NTSR fundamentally changes how we view weed adaptation (Riechers et al., 2024). Compounding the issue, many weed populations now exhibit multiple resistance by

combining both TSR and NTSR, leaving chemical control options severely limited (Hulme, 2022).

In Serbia, herbicide resistance has become a major agronomic problem, particularly in the Vojvodina region, which is characterized by intensive agriculture (Malidža et al., 2022, 2023). The issue dates back to the early 1990s, when Janjić et al. (1992, 1994a, 1994b, 1995) first detected reduced atrazine sensitivity in *Amaranthus retroflexus*. Subsequently, Pavlović et al. (2006, 2007a, 2007b) confirmed declining susceptibility to PSII inhibitors in *Abutilon theophrasti*.

This escalating problem stems from a long-term reliance on herbicides with identical MoA, notably ALS and ACCase inhibitors (Vrbničanin, 2020; Malidža et al., 2022, 2023). The Vojvodina agroecosystem presents a high risk for resistance development due to crop rotations dominated by maize, soybean, sunflower, and wheat, combined with repeated chemical applications. Farmers have overused ALS inhibitors due to their low cost and broad-spectrum efficacy, inadvertently accelerating selection pressure. This focus on chemical weed control, combined with a lack of non-chemical alternatives, has enabled the rapid spread of resistance (Vrbničanin et al., 2020).

Today, multiple resistance actively threatens the control of several key weed species across Serbia, such as *Sorghum halepense*, *Ambrosia artemisiifolia*, *Echinochloa crus-galli*, and *Datura stramonium*, along with resistant populations of *Amaranthus retroflexus*, *Chenopodium album*, and *Helianthus annuus* (Božić et al., 2007, 2011; Malidža et al., 2014, 2015, 2017, 2018). The spread of these biotypes directly threatens the stability of major cropping systems. Managing this problem requires a shift toward IWM, particularly through diversified crop rotations, the use of herbicides with different mechanisms of action, and non-chemical control methods to preserve herbicide efficacy (Vrbničanin, 2020; Malidža et al., 2022, 2023).

EU regulatory pressure and reduction of herbicide availability. The intensive and long-term use of herbicides in modern agricultural systems has led to increasing scientific and public concern regarding their potential adverse effects on human health and the environment. Recent studies highlight that large-scale and repeated herbicide applications contribute to the contamination of soil and water resources, disrupt ecosystem processes, and may negatively affect biodiversity, particularly through the loss of plant community heterogeneity and indirect impacts on non-target organisms (Silva et al., 2019; Tang et al., 2021; Bacmaga et al., 2024). In parallel, concerns about chronic human exposure via occupational contact, food residues, and environmental pathways have further intensified the need for more comprehensive risk evaluation frameworks. These cumulative risks, closely linked to the intensification of herbicide use, have prompted increasing demands for stricter oversight of their registration, application, and distribution. Consequently, regulatory systems, most notably within the European Union, have undergone significant tightening by adopting highly precautionary and hazard-based approaches. This shifting regulatory landscape has led to a progressive reduction in available chemical weed control options, as numerous active substances fail to meet renewed registration criteria (European Commission, 2020; Kudsk and Mathiassen, 2020; Möhring et al., 2020). Despite these challenges, herbicides remain indispensable components of modern weed

management, particularly in large-scale production systems; however, their long-term sustainability increasingly depends on integration with complementary non-chemical approaches.

Herbicide regulation within the European Union has become progressively more restrictive over the past two decades, reflecting an increasing emphasis on environmental protection, food safety, and human health. Anchored by Regulation (EC) No 1107/2009, the European regulatory framework for plant protection products is widely considered one of the most stringent in the world (European Parliament and Council, 2009; Kudsk and Mathiassen, 2020). These regulations profoundly shape agricultural practices within EU member states (Möhring et al., 2020). Furthermore, they exert a significant global impact, often structuralized as the „Brussels effect”, influencing international pesticide development, trade standards, and agricultural policies worldwide.

Regulatory changes within the European Union have substantially reshaped the landscape of herbicide availability and use, with significant implications for farmers, agrochemical industries, and weed management strategies. Over the past decade, increasingly stringent regulatory frameworks, particularly under Regulation (EC) No 1107/2009 and the Farm to Fork Strategy, have led to the progressive withdrawal or restriction of numerous herbicide active substances due to concerns regarding environmental persistence, ecotoxicity, and human health risks (Silva et al., 2019; European Commission, 2020; Kudsk and Mathiassen, 2020). Available estimates indicate that the number of approved herbicide active substances in the EU has declined substantially, from approximately 350–400 in the early 1990s to around 160–180 in recent years (Table 2). The most pronounced decline occurred during the implementation of Directive 91/414/EEC, when many older herbicides failed to meet updated toxicological and environmental criteria. Subsequent regulatory tightening under Regulation (EC) No 1107/2009 has sustained this downward trend, particularly through the application of hazard-based cut-off criteria and periodic renewal assessments (Kraehmer et al., 2014; Kudsk and Mathiassen, 2020). As a consequence, the number of available chemical options for weed control has declined, reducing the diversity of herbicide MoA accessible for application (Figure 2) (Kraehmer et al., 2014; Heap, 2026). This contraction in the herbicide toolbox can significantly increase the complexity, cost, and uncertainty of weed management, particularly in intensive cropping systems where chemical control has historically been dominant (Barker et al., 2023; Travlos et al., 2023).

Table 2. Temporal trend in the number of approved herbicides in the EU.

~1993	~350–400	Pre-Directive 91/414/EEC	Wide range of legacy herbicides on the market
2001–2003	~300–320	Start of Directive 91/414/EEC	Initial screening and data requirements eliminate weaker dossiers
2008–2009	~220–250	Completion of Directive 91/414/EEC	Major reduction following EU-wide reassessment
2011	~200–220	Regulation (EC) 1107/2009 enters into force	Introduction of hazard-based cut-off criteria
2015	~180–200	Renewal phase under 1107/2009	Continued gradual decline
2020	~170–190	Farm to Fork Strategy adopted	Policy-driven pressure for further reductions

2023–2025 ~160–180

Current regulatory phase

Ongoing non-renewals (e.g., diquat, linuron,
etc.)

Beyond the overall reduction in the number of herbicide active substances, EU regulatory processes have also led to a significant contraction in the diversity of herbicide MoA availa-

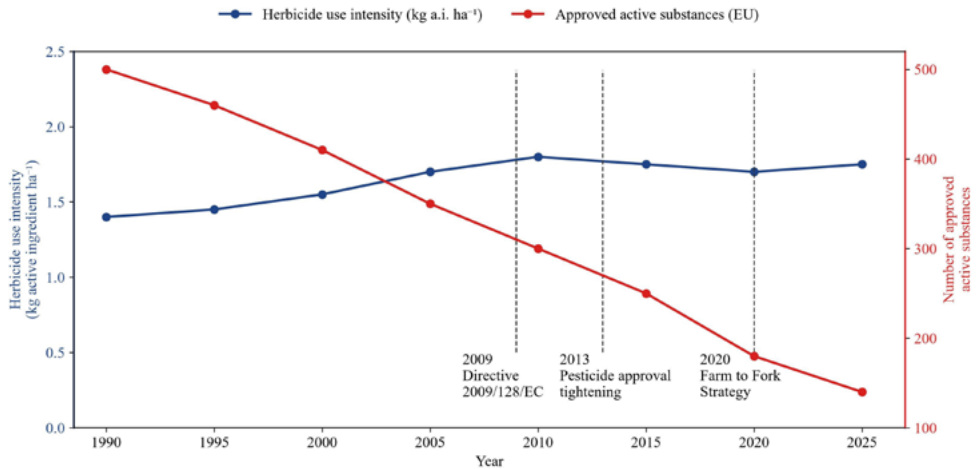


Figure 2. Trends in EU herbicide use intensity relative to the number of approved active substances (1990–2025).

ble for weed control. This loss is unevenly distributed across HRAC groups, with some MoA categories being disproportionately affected. For instance, photosystem II inhibitors (5/C1C2 HRAC group) and photosystem I herbicides (2/D HRAC group) have experienced substantial declines due to the non-renewal of key active substances such as linuron, isoproturon, and diquat. Similarly, the non-renewal of glufosinate has reduced the availability of glutamine synthetase inhibitors (10/H HRAC group), limiting alternatives to glyphosate in non-selective weed control. In contrast, certain MoA groups, including ALS inhibitors (2/B HRAC group), ACCase inhibitors (1/A HRAC group), and synthetic auxins (4/O HRAC group), remain available but are increasingly relied upon, thereby elevating the risk of resistance evolution (Kraehmer et al., 2014; Barker et al., 2023).

Notably, the limited introduction of new herbicide MoA over the past three decades has further exacerbated this issue. The discovery and commercialization of novel herbicide MoA have slowed considerably since the 1980s due to high development costs, increasingly stringent regulatory requirements, and scientific challenges associated with identifying new MoA (Duke, 2012). Consequently, the regulatory withdrawal of existing herbicides is not being offset by sufficient chemical innovation, resulting in a decline in the functional diversity of herbicides alongside a numerical reduction in active substances. This trend constrains the ability to design effective herbicide rotation and mixture strategies and increases reliance on a progressively narrower range of available MoA (He et al., 2022; Barker et al., 2023; Duke et al., 2024).

These developments have critical implications for resistance management, as the availability of multiple MoAs is a cornerstone of sustainable weed control. The disproportionate loss of certain MoA groups may lead to over-reliance on the remaining herbicides, accelerating the selection of resistant weed populations (Barker et al., 2023; Heap, 2026). In this context, allelopathy and allelopathy-based cropping strategies are increasingly viewed as complementary tools capable of enhancing weed suppression while reducing dependence on increasingly limited herbicide options and mitigating selection pressure for herbicide resistance (Travlos et al., 2023).

AGROECOLOGICAL ALTERNATIVES TO HERBICIDE DEPENDENCE

The widespread evolution of herbicide resistance in weed populations demands a transition toward agroecological management practices (Harker and O'Donovan, 2013; Gerhards et al., 2024). Instead of applying synthetic herbicides for weed control, agroecological systems are structured to enhance the natural suppressive capacity of the crop environment (Bommarco et al., 2013). Integrating non-chemical weed control measures, such as diverse crop rotations, competitive cultivars, and altered sowing dates, directly disrupts weed establishment and growth (MacLaren et al., 2020). These practices modify the field microclimate and soil conditions, which inhibit weed development, deplete the weed seedbank, and enhance long-term agroecosystem resilience (Simić et al., 2016; Tamburini et al., 2020).

IWM provides the foundational framework for this approach (Harker and O'Donovan, 2013). Combining mechanical cultivation, agronomic practices, and biological control measures targets weed communities through multiple mechanisms of suppression (Kaur et al., 2024). This diverse management regime prevents weed communities from shifting toward dominance by a few problematic, well-adapted species (Adeux et al., 2022). As a result, weed suppression functions as a continuous, system-level process that maintains overall agrobiodiversity, avoiding the intense selection pressure imposed by repeated herbicide applications.

Harnessing biological processes within ecologically intensified fields strengthens weed regulation (Scavo and Mauromicale, 2021). This approach manages crop–weed interactions to decrease weed emergence and reduce growth rates (Inderjit et al., 2011). While sustainable weed suppression relies heavily on resource competition, allelopathy offers a distinct biochemical advantage (Gerhards et al., 2024). This process utilizes natural compounds to directly inhibit the germination and development of competing species. Consequently, these plant-to-plant biochemical interactions provide the foundation for the agroecological approaches that the following chapter will analyze.

ALLELOPATHY-BASED WEED MANAGEMENT STRATEGIES

The growing limitations of synthetic herbicides, particularly the rapid spread of herbicide-resistant weed populations and rising environmental and human health concerns, have intensified interest in ecologically based weed management approaches. In this context, allelopathy has emerged as an important component of IWM, offering strategies that use plants and their bioactive compounds to suppress weed establishment, growth, and reproduction (Khamare et al., 2022). Principal allelopathy-based weed management strategies include allelopathic cover crops, intercropping systems, crop rotation, and mulching with allelopathic plant residues. In the following sections, the allelopathic effects of aqueous extracts and essential oils, as well as the potential use of allelochemicals as natural herbicides, will be discussed separately.

Cover crops are among the most extensively studied agroecological tools for reducing herbicide dependence in modern cropping systems. Their weed-suppressive effects result from a combination of physical competition, rapid canopy closure, residue mulching, and biochemical interference through allelopathy (Osipitan et al., 2019; Fernando and Shrestha, 2023). Species such as cereal rye (*Secale cereale*), sorghum (*Sorghum bicolor*), and Brassicaceae crops are particularly effective because they release allelochemicals, including sorgoleone and glucosinolate-derived isothiocyanates, which inhibit weed germination and early seedling growth (Farooq et al., 2011; Šćepanović et al., 2021; Khamare et al., 2022). In the majority of cropping systems, suppressive effects of allelopathy are closely associated with other mechanisms, particularly residue-mediated inhibition and competition for light, water, and nutrients, collectively contributing to significant reductions in weed emergence and biomass (Mahé et al., 2022). Furthermore, cover crop mixtures, especially cereal-legume combinations, often provide more stable and persistent weed suppression due to the complementary effects of mulch production, resource competition, and allelopathic activity (Samarajeewa et al., 2006; Tursun et al., 2018; Mennan et al., 2020).

Intercropping systems contribute to sustainable weed management by enhancing crop competitiveness and promoting allelopathic interactions within diversified plant communities. The simultaneous cultivation of two or more crop species improves resource-use efficiency and reduces the ecological space available for weeds (Liebman and Dyck, 1993). In many cases, the inclusion of allelopathic species enhances weed suppression by releasing bioactive compounds that interfere with weed germination and growth (Baumann et al., 2002). Studies involving sorghum, legumes, sesame, canola, and clover-based intercrops have demonstrated significant reductions in weed density and biomass while maintaining or improving crop productivity (Iqbal et al., 2009; Rad et al., 2020). Additional research has shown that cereal-legume combinations frequently improve both yield stability and weed suppression efficiency (Bulson et al., 1997; Vrignon-Brenas et al., 2018). However, the magnitude of allelopathic effects depends largely on species composition, cropping practices, and environmental conditions, indicating that optimized crop combinations are necessary to achieve consistent agronomic benefits.

Crop rotation remains a fundamental agroecological practice for disrupting weed life cycles and reducing the selection pressure associated with continuous herbicide use (Peters et al., 2003; Farooq et al., 2011). The incorporation of allelopathic crops into rotational systems enhances weed suppression by releasing phytotoxic compounds from roots and decomposing plant residues. Species such as sorghum, rye, sunflower, pearl millet, and buckwheat have demonstrated considerable potential to suppress weeds (Mahé et al., 2022). Rotational diversity also modifies sowing dates, crop architecture, and resource availability, thereby limiting the adaptation of weed communities to a single production system (Peters et al., 2003). In some cases, allelopathic effects may persist in the soil beyond the growing season, contributing to longer-term suppression of weed emergence, as demonstrated in studies involving allelopathic rice cultivars and the suppression of *Sorghum halepense* (Dmitrović et al., 2015). Nevertheless, the success of allelopathic rotations is highly context-dependent, as negative carryover effects on subsequent crops have occasionally been reported, particularly in sorghum-wheat and rye-maize systems (Raimbault et al., 1990; Ben-Hammouda et al., 1995). Therefore, careful design of crop sequences and species selection is essential to maximize weed control while minimizing adverse agronomic interactions.

Mulching with allelopathic plant residues represents an effective strategy for integrating physical weed suppression with biochemical interference. Organic mulches suppress weeds by limiting light penetration, forming mechanical barriers to emergence, and modifying soil moisture and temperature conditions (Teasdale and Mohler, 2000; Richardson et al., 2008; Marble, 2015). In addition, residues from allelopathic species release water-soluble phytotoxic compounds during decomposition, further inhibiting weed germination and seedling development (Chalker-Scott, 2007). Plant residues derived from sorghum, sunflower, wheat, rice, eucalyptus, and brassicas have shown substantial inhibitory effects on a wide range of weeds under both laboratory and field conditions (Singh et al., 2003; Cheema et al., 2004; Mahmood and Cheema, 2004). Eucalyptus residues and extracts, in particular, have been widely documented for their phytotoxic activity against sensitive species (Kohli and Singh, 1991; Molina et al., 1991). Moreover, mixtures of allelopathic residues often provide stronger weed suppression than single-species mulches due to synergistic interactions among different allelochemicals (Khan et al., 2004). Beyond weed control, residue mulching contributes to soil conservation, organic matter accumulation, enhanced microbial activity, and improved water retention, reinforcing its importance within sustainable agricultural systems (Tiquia et al., 2002).

Application of allelopathic water extracts and essential oils. Plant water extracts and essential oils constitute two major sources of secondary metabolites that function as natural allelochemicals. Chemically, aqueous extracts consist mainly of hydrophilic phenolic acids, flavonoids, and glycosides, while essential oils are characterized by lipophilic (non-polar) fractions, principally monoterpenes and sesquiterpenes (Czarnota et al., 2003; Đorđević et al., 2019; Khamare et al., 2022). These diverse allelochemicals influence weed germination and growth through multiple physiological and biochemical mechanisms (Tsao et al., 2002;

Azhar et al., 2010; Kim et al., 2015). For instance, members of the *Sorghum* genus release hydrophilic phenolic acids and their aldehyde derivatives, alongside the hydrophobic compound sorgoleone. The water fraction of sorghum extracts has demonstrated significant phytotoxic effects against several weed species, including *Chenopodium album*, *Rumex dentatus*, and *Convolvulus arvensis* (Czarnota et al., 2003; Cheema et al., 2004). Consistently, aqueous extracts from various other plant species exhibit a similar phytotoxic mechanism mediated by water-soluble polyphenols, most notably flavonoids such as rutin and (+)-catechin, alongside p-coumaric and caffeoylquinic acids. Extracts derived from species such as *Asclepias syriaca*, *Juglans regia*, *Abutilon theophrasti*, and *Ambrosia artemisiifolia* consistently disrupt core metabolic pathways, thereby inhibiting seed germination, drastically reducing photosynthetic pigment content, and inducing severe oxidative stress in target weeds such as *Amaranthus retroflexus* and *Chenopodium album* (Đorđević et al., 2022; Gajić Umiljendić et al., 2022, 2025). Similarly, the tree of heaven (*Ailanthus altissima*) contains a diverse array of bioactive compounds, including alkaloids, terpenoids, steroids, flavonoids, phenolics, and quassinoids (Albouchi et al., 2013; Kim et al., 2015; Ni et al., 2018). Aqueous leaf extracts of this species have been shown to inhibit germination and early growth in crops such as alfalfa (Tsao et al., 2002). Extracts from eucalyptus leaves likewise exhibit strong inhibitory effects, reducing seed germination and biomass accumulation in maize (Khan et al., 2004).

While individual plant extracts can provide measurable weed suppression, increasing evidence indicates that combinations of allelopathic extracts may produce enhanced or synergistic effects. For example, the joint application of sorghum, sunflower, and eucalyptus extracts achieved approximately 70% weed control, exceeding the efficacy of single-species extracts (Cheema et al., 2003). Likewise, combined sorghum and sunflower extracts reduced the growth of *Trianthema portulacastrum* by approximately 66% (Azhar et al., 2010).

An additional advantage of these bio-based approaches is their compatibility with reduced herbicide inputs. Several studies have shown that integrating allelopathic extracts with sublethal herbicide doses can maintain or even improve weed control efficacy. For example, applying an aqueous extract of *Cuscuta campestris* stems together with a reduced dose of metribuzin increased control of *Amaranthus retroflexus* and *Portulaca oleracea* compared with metribuzin alone (Sarić-Krsmanović et al., 2023). Similarly, combining aqueous extracts of *Ambrosia artemisiifolia* or *Xanthium strumarium* with a reduced dose of mesotrione induced a strong allelopathic response that suppressed weed biomass by over 90% and reduced photosynthetic pigments by 80% in *Abutilon theophrasti* and *Chenopodium album* (Sarić-Krsmanović et al., 2021).

In recent years, significant research has focused on the herbicidal and phytotoxic efficacy of plant essential oils as sustainable alternatives for weed control. Monoterpene-rich essential oils have been demonstrated to possess potent bioherbicidal properties, though their practical application is often constrained by a lack of selectivity toward cultivated crops. For instance, the essential oil of *Anethum graveolens* exhibited remarkable suppression of the parasitic weeds *Cuscuta campestris* and *Cuscuta epithymum*, achieving up to 100% inhibition of seed germination and seedling growth at concentrations ranging from 0.01-1%,

while inducing severe phytotoxicity in host crops such as red clover (*Trifolium pratense*) and alfalfa (*Medicago sativa*) (Sarić-Krsmanović et al., 2023). Similarly, the essential oil of common thyme (*Thymus vulgaris*), dominated by carvacrol and thymol, achieved absolute (100%) inhibition of *Abutilon theophrasti* seed germination at a 1% concentration. Recent advancements in bioherbicide technology have further confirmed that specific oxygenated terpenes, such as 1,8-cineole and α -pinene, disrupt core physiological mechanisms, including photosynthesis and cellular respiration, inducing severe oxidative stress in target weeds (Verdeguer et al., 2020a, 2020b). To overcome sensitivity to environmental factors, recent studies utilizing 1% nanoemulsions of cinnamon (*Cinnamomum verum*) and clove (*Syzygium aromaticum*) essential oils demonstrated over 90% desiccation and leaf necrosis in *Agropyron repens* and *Bromus* spp. within seven days, primarily through marked suppression of superoxide dismutase activity and cellular membrane disruption (Azizi et al., 2025). Furthermore, investigations into the allelopathic potential of invasive species showed that essential oils extracted from *Ambrosia trifida* exert heavy phytotoxic pressure on horticultural crops, significantly hindering the early development of lettuce, watermelon, tomato, and cucumber (Sarić-Krsmanović et al., 2020). Collectively, these findings underscore that while essential oils offer high efficacy in disrupting weed physiology, their commercial adoption as bioherbicides requires careful dose optimization and targeted application strategies to mitigate non-target damage to cash crops.

Overall, the utilization of aqueous plant extracts and essential oils represents a promising and environmentally sustainable component of integrated weed management strategies. Their application, either alone or in combination with conventional herbicides, offers the potential to reduce chemical inputs, mitigate the development of herbicide resistance, and exploit the vast diversity of naturally occurring allelochemicals across plant species.

Allelochemicals as potential natural herbicides. Growing awareness of the environmental and toxicological limitations of conventional herbicides, coupled with the persistent lack of new herbicide MoA and the accelerating global spread of herbicide-resistant weed populations, has intensified the search for alternative, biologically based weed management strategies (Duke et al., 2000). Plant-derived secondary metabolites, or allelochemicals, offer a broad range of chemical structures capable of disrupting key physiological and biochemical processes in plants (Hasan et al., 2021; Scavo and Mauromicale, 2021). These compounds encompass diverse chemical classes, such as phenolics, terpenoids, alkaloids, quinones, flavonoids, and benzoxazinoids (Đorđević et al., 2019; Khamare et al., 2022). Their ecological role, however, extends beyond simple plant–plant interference to encompass broader interactions within the soil and microbial communities. In addition to their ecological functions, these compounds serve as valuable blueprints for herbicide discovery. They have helped identify new molecular targets and guided the synthesis of several modern commercial herbicides (Khamare et al., 2022; Berestetskiy, 2023; Kostina-Bednarz et al., 2025).

A well-established example is mesotrione, a triketone herbicide derived from leptospermone, a natural phytotoxin originally isolated from the roots of *Callistemon citrinus* (Mitchell et al., 2001). Mesotrione acts by inhibiting HPPD, an enzyme identified through these early

studies on natural triketones. This discovery is widely cited as a benchmark for successfully translating natural phytotoxicity into synthetic herbicide design (Mitchell et al., 2001; Jhala et al., 2022). Leptospermone, which is also a major constituent of *Leptospermum scoparium* essential oil (van Klink et al., 1999), subsequently served as the structural template for other commercial analogues, such as sulcotrione (Dayan et al., 2003). Similarly, cinmethylin represents an early shift from natural compounds to herbicide design, being derived from the monoterpene 1,4-cineole, a common essential oil component with inherent phytotoxic properties (Einhellig and Leather, 1988). These precedents highlight how natural products continue to guide modern herbicide chemistry, offering novel MoA to resolve cross-resistance issues (Berestetskiy, 2023; Kostina-Bednarz et al., 2023). However, candidate allelochemicals differ substantially in their chemical structures, physiological targets, and environmental persistence, complicating their standardization in agronomic systems. The vast biochemical and functional diversity of these plant-derived compounds, many of which show strong herbicidal potential by attacking multiple pathways simultaneously, is illustrated in Table 3.

Table 3. Allelochemicals with potential for herbicide development.

Chemical class	Natural compound	Botanical source	Proposed mode(s) of action
Triketones	Leptospermone	<i>Callistemon citrinus</i>	Inhibition of HPPD enzyme; disruption of carotenoid biosynthesis.
Terpenoids	1,8-Cineole	<i>Eucalyptus</i> spp., <i>Salvia</i> spp.	Mitotic inhibition and root growth suppression; membrane integrity disruption.
Sesquiterpene lactones	Artemisinin	<i>Artemisia annua</i>	Induction of oxidative stress; inhibition of seedling development.
Phenols / Coumarins	Scopoletin	<i>Artemisia vulgaris</i>	Inhibition of seedling growth and interference with photosynthetic electron transport.
Quinones	Sorgoleone	<i>Sorghum</i> spp.	Potent inhibitor of Photosystem II (PSII) and mitochondrial respiration.
Naphthoquinones	Juglone	<i>Juglans</i> spp.	Inhibition of cell division and disruption of mitochondrial function.
Sulfur compounds	Isothiocyanates	<i>Sinapis arvensis</i>	Natural biofumigant; inhibition of seed germination and microbial growth.
Phenolic acids	<i>p</i> -Coumaric acid	<i>Hordeum vulgare</i>	Alteration of membrane permeability and interference with nutrient uptake.
Benzoxazinoids	DIBOA / DIMBOA	<i>Secale cereale</i> , <i>Zea mays</i>	Root growth inhibition; interference with amino acid metabolism.
Alkaloids	Caffeine	<i>Coffea arabica</i>	Inhibition of mitosis; interference with DNA/RNA synthesis.
Flavonoids	Catechins / Quercetin	<i>Centaurea stoebe</i>	Auxin transport inhibition; modification of rhizosphere pH.

Despite growing academic interest and significant research breakthroughs, the commercialization of bioherbicides remains globally limited. This stark disparity between laboratory success and market adoption is highlighted by the few products, primarily specific microbial agents, essential oils, and plant secondary metabolites, that have successfully navigated regulatory approval. In commercial agriculture, the widespread adoption of these natural

solutions is heavily restricted by stringent regulatory frameworks, inconsistent field efficacy, and the technical challenges of ensuring formulation stability and quality control during mass production (Macías et al., 2019; Verdeguer et al., 2020; Kostina-Bednarz et al., 2025).

Compounding these challenges, natural herbicides often require higher application rates than their synthetic counterparts to achieve comparable efficacy. These elevated doses inflate production costs and risk harming non-target organisms, particularly soil microbial communities, an ecological impact that remains largely overlooked during initial screening phases. Furthermore, many existing formulations exhibit broad-spectrum, non-selective activity, reducing their utility in cropping systems that demand strict crop safety. To circumvent these limitations, recent advances in nanoformulations, encapsulation technologies, and controlled-release delivery systems aim to stabilize these compounds and enhance their persistence under field conditions (Pérez-de-Luque, 2024; Jayasoorya and Kumar, 2024). Increasingly, research shifts toward synergistic strategies that combine allelochemicals with reduced herbicide doses or cover crops (Kostina-Bednarz et al., 2023), thereby establishing integrated weed management as a cornerstone of sustainable agronomy.

Within this framework, bioherbicides are better understood as integral components of integrated weed management rather than direct substitutes for synthetic chemistry. Their most realistic value lies in complementing existing control strategies within diversified agronomic systems, particularly in contexts where reducing chemical inputs and managing resistance are priorities. Crucially, the limitations of these approaches stem not from a lack of biological activity but from deficits in ecological reliability, formulation technology, and field-scale consistency. Future progress will therefore depend on effectively translating these known bioactive compounds into stable, selective, and scalable delivery systems, rather than simply discovering new allelochemicals. To achieve reliable performance under heterogeneous field conditions, this transition must combine advanced formulation technologies and agroecological practices with precision agriculture tools (MacLaren et al., 2020; Jayasoorya and Kumar, 2024; Kostina-Bednarz et al., 2025).

INTEGRATION OF ALLELOPATHY INTO SUSTAINABLE WEED MANAGEMENT

Placing allelopathy within the framework of IWM highlights its true value for sustainable agriculture, especially under rising environmental, regulatory, and technological pressures. In practice, weed management is no longer stable enough to rely on single control mechanisms without quickly running into resistance problems and long-term system instability. Because of this, IWM is shifting toward a combination of biological, chemical, mechanical, and digital approaches that act together rather than independently (Travlos et al., 2023; Jahanbakht et al., 2026). Within this broader shift, allelopathy functions as a context-dependent ecological process that adds another layer of functional diversity to weed suppression (Khamare et al., 2022; Kostina-Bednarz et al., 2023).

Unlike conventional weed management tools, allelopathy operates as a system regulator rather than a direct control method. It functions by modulating overall agroecosystem behavior through interactions between crop species, residue decomposition, soil microbiology, and weed population density and distribution (Kostina-Bednarz et al., 2023). While it seldom provides standalone weed control, this ecological process ultimately determines the necessity and intensity of subsequent management practices.

Mitigating herbicide dependency is a primary catalyst for implementing allelopathic strategies. Repeatedly applying chemical treatments with identical modes of action has triggered widespread weed resistance (Scavo and Mauromicale, 2021; Arora et al., 2024). Allelopathic crops, cover crops, and residue management introduce alternative suppression pathways that operate independently of traditional herbicide target sites, thereby countering this resistance pressure. By diversifying selection pressure, these ecological systems stall resistance development and fortify the overall effectiveness of weed control programs (Scavo and Mauromicale, 2021; Travlos et al., 2023; Arora et al., 2024).

Concurrently, precision agriculture technologies amplify the relevance of allelopathic strategies. Leveraging spatial weed mapping, UAV-based imaging, and AI-driven detection systems transitions weed management toward site-specific execution (Jahanbakht et al., 2026; Wang et al., 2026). Recent advances in deep learning and remote sensing enable weed detection and mapping at ultra-fine spatial scales, unlocking opportunities for highly targeted interventions (Yang et al., 2023; Garcia-Martinez et al., 2023; Upadhyay et al., 2024). In principle, these technological milestones dynamically align allelopathic interventions with within-field variability, even though such integration remains primarily conceptual rather than fully operational.

Despite these technological strides, a profound disconnect persists between digital detection systems and biological weed suppression strategies. Current precision management tools focus almost exclusively on immediate, reactive chemical or mechanical elimination (Ahmadi et al., 2023; Upadhyay et al., 2024). Consequently, they fail to leverage slower, biologically mediated dynamics like allelopathy. Furthermore, operational constraints, including processing limitations, sensor resolution, and real-time computational demands, restrict the integration of ecological complexity into field-scale systems (Ahmadi et al., 2023; Wang et al., 2026). This misalignment between hardware capability and ecological understanding remains a primary bottleneck in sustainable agriculture.

From a broader agroecosystem perspective, allelopathy supports multiple agroecological functions within regenerative agriculture (Schulz and Tabaglio, 2024). By simultaneously targeting weed suppression, soil organic matter dynamics, and microbial activity, allelopathic systems enhance both nutrient cycling and soil structure. However, these multi-functional benefits are highly sensitive to local ecological parameters. In practice, site-specific soil biology and the rapid decomposition or transformation of allelochemicals dictate outcomes, causing significant variation between fields and across seasons (Mahé et al., 2022; Kostina-Bednarz et al., 2023).

Beyond digital integration, the relevance of allelopathy extends directly into climate-smart agriculture, where it indirectly mitigates environmental impacts. By reducing synthetic

herbicide reliance, enhancing soil cover, and minimizing erosion risks, allelopathic systems substantially decrease energy inputs. Consequently, they lower greenhouse gas emissions fundamentally tied to herbicide manufacturing and application. However, these ecological dividends are not intrinsic traits of allelopathy per se; rather, they depend strictly on comprehensive system design and adaptive management frameworks (Khamare et al., 2022; Kostina-Bednarz et al., 2023).

Despite its potential, the operational volatility of allelopathy under field conditions remains a critical limitation (Scavo and Mauromicale, 2021; Mahé et al., 2022). Soil properties, microbial dynamics, climatic fluctuations, and residue decomposition rates collectively govern the persistence and efficacy of allelochemicals. This environmental dependency severely complicates predictability, hindering the direct translation of controlled laboratory findings into commercial agroecosystems (Kostina-Bednarz et al., 2023). Consequently, allelopathy is an environment-dependent process rather than a reliable standalone weed control method.

From a broader perspective, the primary value of allelopathy lies not in providing standalone weed control but in expanding the diversity of suppression mechanisms within IWM frameworks. Broadening the range of eco-physiological processes acting upon weed populations enhances system resilience against both biological adaptation and environmental variability (Scavo and Mauromicale, 2021). This approach aligns with the ongoing transition toward knowledge-intensive, ecologically grounded weed management, where long-term outcomes depend on complex system interactions rather than isolated single interventions.

Ultimately, embedding allelopathy within IWM, precision technology, regenerative practices, and climate-smart agriculture drives the transition toward adaptive, multifunctional weed management systems. Its core value shifts the focus away from mechanical consistency, emphasizing instead structural diversity, reduced synthetic reliance, and long-term ecosystem stability. As insights into plant–plant chemical communication expand alongside digital innovations, allelopathy will become a fully operational tool in sustainable agriculture. However, its practical success will always depend on and be limited by the specific environmental context.

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Alelopatija i održivo upravljanje korovima u doba rezistentnosti na herbicide i zakonskih ograničenja

REZIME

Decenijama unazad, hemijsko suzbijanje korova ima ključnu ulogu u poljoprivredi, obezbeđujući efikasno suzbijanje i potrebnu produktivnost useva. Višegodišnja, učestala primena herbicida sa istim mehanizmom delovanja ubrzala je razvoj rezistentnih biotipova korova. Danas je ovaj agronomski izazov dodatno otežan strogom zakonskom regulativom Evropske unije, kojom su drastično ograničene dostupne hemijske mere suzbijanja korova usled sistematskog povlačenja aktivnih supstanci sa tržišta. Zbog toga je primena nehemijskih metoda u okviru integralnog upravljanja korovima postala imperativ za dugoročno održivu proizvodnju hrane. U tom kontekstu, alelopatija predstavlja prihvatljiv agroekološki pristup koji koristi biljke i njihove bioaktivne supstance-alelohemikalije za suzbijanje korovskih vrsta. U okviru ovog preglednog rada razmatraju se agroekološke alternative koje bi mogle da smanje zavisnost od herbicida, sa

posebnim fokusom na primenu alelopatskih vodenih ekstrakata i etarskih ulja, a posebno se analizira potencijal alelohemikalija kao prirodnih herbicida. Integrisanje alelopatije u okvire integralnog suzbijanja korova pomera težište sa hemijskog suzbijanja korova ka novim strategijama. Istraživanja su pokazala da se uvođenjem alternativnih bioloških pristupa suzbijanju korova može diversifikovati selekcionni pritisak i usporiti razvoj rezistentnosti. Uspješna integracija ovih strategija u savremenu poljoprivrednu proizvodnju može značajno smanjiti zavisnost od herbicida i unaprediti stabilnost agroekosistema.

Ključne reči: rezistentnost korova na herbicide, regulativa Evropske unije, alelopatija, prirodni herbicidi, integralno suzbijanje korova.