Indian Journal of Weed Science (2022) **54**(4): 389–396
http://dx.doi.org/10.5958/0974-8164.2022.00070.3

REVIEW ARTICLE

Bioavailability of allelochemicals in soil environment under climate change: Challenges and perspectives

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Received: 20 October 2022 | Revised: 1 November 2022 | Accepted: 7 November 2022

ABSTRACT

Weed management is an important component in sustainable agriculture. The current agriculture is changing with climate change. Allelopathy has been recognized as a component of integrated weed management over the years. The allelopathic ideas have been used in various facets of allelopathic implications. Some of these include use of cover crops, plant residues, plant extracts, crop cultivars and others. And it is being challenged under climate change factors such as increased atmospheric CO_2, temperature rise, erratic rainfall patterns and others. The relevance of allelopathy has been highly discussed due to the lack of phytotoxic concentrations of allelochemicals under field conditions. Crop residues from existing crop or rotational crops can provide selective weed suppression through their physical presence on the soil surface and/or through the release of allelochemicals. *Brassica nigra*, *Avena fatua*, *Fagopyrum esculentum*, *Secale cereale*, *Sorghum bicolor, Triticum aestivum* and other cover crops have been used in weed management on a limited basis. Some of the allelochemicals such as DIBOA, DIBOA-glycoside, dhurrin, isoflavonoids, isothiocyanate, juglone, momilactone, scopoletin, and sorgoleone have been reported to play a role in weed management under field conditions. The living and dynamic soil system influences the fate and functions of allelochemical activity. The bioavailability of allelochemicals in the soil is dependent on soil processes such as adsorption, leaching and degradation by abiotic and biotic factors. These processes and other related soil conditions are greatly influenced by several underlined climatic variables. Future allelopathic research should be focused on persistence and availability of allelochemicals in soil environment. The bioavailability of allelochemicals under field conditions with climate change associated rising atmospheric CO_2, rising temperature and intensity and erratic rainfall must be established for its effective practical role in weed management. Currently, we face challenges and opportunities in using allelopathy as a part of weed management strategies in today's agriculture.

Keywords: Allelopathy, Adsorption, Climate change, Cover crops, Crop residue, Microbial activity

INTRODUCTION

Allelopathy has been recognized, over the years, as a component of integrated weed management (IWM). The role of allelopathy has been reported in the usage of components of IWM such as the use of cover crops, plant residues, plant extracts, crop cultivars and others. Scavo and Mauromicale (2021) reviewed the role of crop allelopathy for sustainable weed management. It is a challenge to utilize allelopathy in future IWM strategies as a component under the times of climate change with increased atmospheric CO_2 and temperature, erratic rainfall patterns of rainfall and others.

The process of allelopathy is difficult to prove in nature in the agricultural fields as it is influenced by many interactive factors. Once a allelochemical is released to soil, all the chemicals can be adsorbed by soil components or transformed by soil microorganisms into less or even more harmful molecules for plants (Kobayashi *et al*. 2004, Tharayil *et al*. 2006).

Crop residues using cover crops or rotational crops for weed management in the field is challenging especially during climatic change. Sainju and Alasinrin (2020) reported that long-term cropping system and nitrogen fertilization contributed changes in soil chemical properties and crop yields. The cover crops usage under various cropping systems has limitations such as delayed planting, delayed crop emergence, phytotoxic effects to major crops, and increased pest pressure.

Weed suppression by rye (*Secale cereale* L.) residue on the soil surface in no-tillage system has been documented from 1980's. Weed suppression can be attributed to both the chemical and physical

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influences of rye residue (Fay and Duke 1977, Bhowmik and Doll 1982, Mennan *et al.* 2020).

Earlier reports have shown that weed suppression or control could be achieved by growing cover crops of rye, barley, wheat or sorghum to a height of 40 to 50 cm, and then desiccating the crop by either contact herbicides or winter freezing and then allowing the residue on the surface (Barker and Bhowmik 2001, Mennan *et al.* 2020).

Vicia villosa has been used as a cover crop and has been demonstrated potential use in weed management (Teasdale and Daughtry 1993). Perennial weed control is a challenging part of weed management. Cover crops are not much effective in managing perennial weed species. It is also believed that regrowth of certain perennial weeds may be favored due to far-red light environment under cover crops. Total weed density and biomass were lower in live *Vicia villosa* treatment compared to desiccated *Vicia villosa* plots. Red (660 nm) and far-red (730 nm) light ratio of transmitted light was reduced by 70% in live *Vicia villosa* and by 17% under *Vicia villosa* desiccated by paraquat. They concluded that factors such as light, soil moisture and temperature are responsible for the weed suppression by *Vicia villosa*. The question remains whether residues from crops or cover crops can provide successful weed management (100%) in the field.

The cropping system could be used to improve soil physical properties and suppression of weeds (Naeem *et al.* 2022). The barley-based cropping systems and weed control strategies influence weed infestation, soil properties and barley productivity (Naeem *et al.* (2022). The greengram-barley system with weed free control improved soil characteristics and barley yield over other cropping systems. The use of allelopathic water extracts significantly suppressed weeds and was equally effective as the chemical control.

The allelopathic effects of waste-land weeds on germination and growth of winter crops was reported (Hayyat *et al.* 2020). Lantana species such as *Lantana camara* L. has been studied well in relation to allelopathic activity to crop species and weed species. In a biometric analysis of allelopathic potential, Maity (2020) reported activity of *Lantana* spp. on mimosa seeds. Gindri *et al.* (2020) demonstrated the effect of allelochemicals from *L. camara* on the seed germination of *Avena sativa* L.. Qureshi *et al.* (2021) isolated natural herbicidal compound from *Lantana camara* L.. Mustafa *et al.* (2019) evaluated dominant allelopathic four weeds on germination and seedling growth of six crops. The effects of rhizome extracts from invasive knot weed *Fallpia japonica* and *F. xbohemica* on radish seed germination and root growth (Soln *et al.* 2021). In nature, plant products represent a vast diversity of compounds with a variety of biological activity (Duke *et al.* 2002, Bhowmik and Inderjit 2003, Weston and Duke 2003, Duke 2015). The natural products represent a diverse class of chemical compounds. These allelochemicals will have impact on different species of plants.

This presentation will highlight allelopathy as a component of integrated weed management, importance of soil factors in allelopathic activity, microbial activity, and potential challenges in allelopathy under climate change.

ALLELOCHEMICALS

Allelochemicals - crop cultivars

Crop cultivars have been screened for their differential allelopathic activity for the last several decades (Dilday *et al.* 1998, Gealy *et al.* 2000, Wu *et al.* 2002, Kato- Noguchi *et al.* 2010, Masum *et al.* 2018). This topic could be a separate review article and therefore I will briefly highlight some of the research work. *Avena* spp., *Oryza* spp., *Sorghum* spp. have been studied in detail over the years (Fay and Duke 1977, Rice 1984, Dilday *et al.* 1998, Gealy *et al.* 2000, Duke *et a*l. 2002, Olofsdotter 2001, Czarnota *et al.* 2003, Kato-Noguchi *et al.* 2010, Masum *et al.* 2016, Masum *et al.* 2018) and was reviewed in detail (Bhowmik 2018).

Fifty rice cultivars from Bangladesh have been screened against *Echinochloa crus-galli* (barnyardgrass) and *Echinochloa colona* (jungle rice) by using Equal Compartment Agar Method (Masum *et al.* 2016) and 7 to 37% suppression of *Lactuca sativa*, *Lepidium sativum*, and *Raphanus sativus* was reported. The allelopathy role in integrated weed management in rice was reviewed well (Patni *et al.* 2018).

Allelochemicals - plant extracts

Use of allelochemicals from plant extracts has been researched for weed management in agriculture. In Pakistan, for example, an aqueous extract deriving from sorghum shoots with a 10% concentration is left to ferment for several weeks and is subsequently sprayed post-emergence for weed control. This fermented water extract, known as "*Sorgaab*", reduced weed density and biomass up to 50%, in field trials, depending on the weed species (Cheema *et al.* 2002). The use of allelopathic water extracts significantly suppressed weeds and was equally effective as the chemical control (Naeem *et al.* 2022).

The research on usage of plant extracts for weed management was reviewed (Bhowmik 2018).

Allelochemicals - isolation

Thousands of allelopathic substances have been isolated from plants and their chemical structure has been determined. However, the mode-of-action (MOA) has only been elucidated for a limited number of allelochemicals (Cheng and Cheng 2015). Some of the allelochemicals such as allyl isothiocyanate (*Brassica* sp., black mustard), fatty acids (*Polygonum* spp.), isoflavonoids and phenolics (Trifolium spp., *Melilotus* spp.), phenolic acids and scopoletin (*Avena sativa*), hydroxamic acids (*Triticum* sp.), phenolic acids, dhurrin, and sorgoleone (*Sorghum bicolor*) have been reported for weed control (Duke *et al.* 2002). Duke and his group have shown artimisinin, a sesquiterpenoid lactone, to inhibit the growth of *Amarantus retroflexus*, *Ipomoea lacunosa*, *Artemisia annua* and *Portulaca oleracea*. Mushtaq and Siddiqui (2010) reported that plants belonging to Asteraceae family are the most studied species for allelopathic potential to control weeds in India. Some of the species including *Parthenium hysterophorus*, *Ageratum conyzoides* and others received more attention.

The allelopathic effects of sorghum on weed species was demonstrated (Czarnota *et al.* 2003, Weston *et al.* 2013). Root exudates of 100 cultivars of *Sorghum bicolor* were evaluated for their potency to affect the seed germination and growth of *Amaranthus retroflexus* (Alsaadawi *et al.* 1986). Some cultivars were more toxic than others.

The inhibition of shoot and root growth of *Echinochloa crus-galli* when co- cultured with rice (*Oryza sativa)* seedlings, in a bioassay, was reported (Kato-Noguchi *et al.* 2010). The momolactone A and B were identified in the bioassay medium of all rice cultivars. The concentrations of mamolactone A and B varied from 0.21-1.5 and 0.66-3.8 umol/L, respectively demonstrating the evidence of secretion of these two compounds from all rice cultivars into the medium.

In *Oryza* species, four biologically active compounds, syringaldehyde (4-hydroxy-3,5-dimethoxybenzaldehyde), (-) loliolide, 3*â*-hydroxy-5*á*,6*á*-epoxy-7-megastigmen- 9-one and 3-hydroxy-*â* –ionone, were isolated (Masum *et al.* 2018). The biological activity of these compounds showed that concentration > 10 ìM significantly inhibited the root and shoot growth of *E. crus-galli* seedlings, and the *I*50 (50% growth inhibition) values ranged from 16.03 to 27.23 ìM and 23.94 to 75.49 ìM for root and shoot growth, respectively.

In recent years, allelopathic research has been increased on trees, invasive species in forest areas. Bitchagno *et al.* (2022) found alkaloids as the main component of the extracts from plants in genus *Peganum*, one of the group of plants in the semi-arid regions of the world. These compounds showed significant potential to manage weeds in crops.

Allelochemicals – soil system

The soil is a living and dynamic system. The living system can influence the functions of allelochemicals in time and space. Soil chemical properties are significantly altered by any cropping system through moisture and nutrient uptake and the amount and quality of crop residue (Sainju and Alasinrin 2020, Wozniak 2020). The bioavailability of allelochemicals in the soil is dependent on processes such as adsorption, leaching and degradations by abiotic and biotic factors. The clay types, organic matter, and soil pH can affect the bioavailability of allelochemicals in the soil and the details were revived by Kobayashi (2004).

The soil can adsorb and modify the fate of allelochemicals. For instance, sorgoleone binds strongly to soil colloids because it is a highly lipophilic allelochemical, with a log (log octanol- water partition coefficient) of 6.1 (Trezzi *et al.* 2016). The allelopathic compounds l-3,4dihydrox phenylalanine and catechin are also strongly adsorbed by soil colloids, possibly due to the catechol group present in these molecules (Furubayashi *et al.* 2007).

Reduced allelopathic potential of benzoxazinoid compounds 2-aminophenoxazin-3-one and DIBOA (2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one) have been reported due to their adsorption by soil colloids (Teasdale *et al.* 2012). The chemical compounds that are not adsorbed onto colloids or minerals are usually in the soil solution. Thus, they can be absorbed by plants or leached (Kobayashi 2004, Kong *et al.* 2007, Li *et al.* 2013). Kong *et al.* (2007) reported that flavonoids with a high mobility in the soil profile were less phytotoxic than those with reduced soil mobility with rice plants. Similarly, an analysis of ten potential allelochemicals revealed an inverse relationship between soil mobility and their toxic effect on target plants (Li *et al.* 2013).

Tharayil *et al.* (2006) demonstrated the role of preferential sorption to soil in altering the chemical composition of plant exudates in a silt loam soil using representative mixtures of plant phenolic acids, namely, hydroxybenzoic acid, vanillic acid, coumaric acid, and ferulic acid. Removal of organic matter substantially decreased the sorption affinity of all phenolic acids. The soil sorption properties of some individual allelochemicals have previously been studied. A detailed description of preferential sorption to soil has been reported and reviewed (Bhowmik 2018).

Gimsing *et al*. (2009) reported mineralization of the allelochemical sorgoleone in soil. Wei et al. (2017) reported soil microbial utilization, enzyme activities and nutrient availability responses to *Biden Pilosa*.

The allelopathy of *Imperata cylindica* may support the invasiveness of the species (Kato-Noguchi 2021). Kato-Noguchi (2022) reported root exudate of *Imperata cylindrica* released into the rhizosphere and surrounding environments containing allelochemical that can alter the microbial community.

The role of sorption to soil in modifying the bioavailability of components in complex allelochemical mixtures is still not well understood. Soils can alter the phytotoxicity of plant secondary metabolites by changing their bioavailability, persistence, and fate under field conditions. Sorption is one of the prominent factors affecting the phytoavailability of allelochemicals in soil.

Allelochemicals - microbial activity

The fate of allelopathic compounds in soil may be altered by soil microorganisms. Phenolic acids are readily converted from one structure to another with different phytotoxicities (e.g., ferulic acid to vanillic acid) by soil-borne microbes (Blum 1998, Inderjit 2001, 2005). Schmidt and Ley (1999) suggested that carbon-limited soil organisms would rapidly mineralize phenolic compounds due to their higher energy content on a per weight basis than simple sugars. Zikmundová *et al*. (2002) studied the biotransformation of the phytoanticipins BOA and HBOA by four endophytic fungi isolated from *Aphelandra tetragona*. It was shown that the metabolic pathway for HBOA and BOA degradation leads to o-aminophenol as a key intermediate.

Microbes can deactivate water soluble allelochemicals released soon after cover crop residue incorporation (Jilani *et al*. 2008). As agricultural soils are not sterile, it is important to understand how microbial activity moderates allelopathic potential of cover crop residues (Blum 1998, Inderjit 2005). Mohler *et al*. (2012) showed that unsterilized live soil (*i.e.*, with a natural microbial community) reduces seedling germination rates when cover crop residues are incorporated, and the combined effect of residues and live microorganisms is greater than the effect of either of these components alone.

Allelochemicals in the soil may be degraded and altered, reducing their efficacy. In non-sterilized soil, for instance, DIBOA showed a half-life of 43h. However, 2-aminophenoxazin-3-one (APO), the fungal degradation product of DIBOA, has a low mineralization rate and therefore, a half-life greater than 90 days (Macías *et al*. 2005). In addition, some flavonoid glycoside molecules exuded by rice plants can suffer high mineralization by soil microorganisms, resulting in a glycosylated compound. Flavonoid glycosides and a glycoside have a half-life of 2 h and 30 h, respectively, suggesting a higher allelopathic activity for the second group (Kong *et al*. 2007). The biodegradation of the sorgoleone quinone ring is relatively slow, with only 21% being mineralized 77 d after incubation in soil. However, the sorgoleone methoxy group was biodegraded within a few days, particularly in soils with a low colloid content (Gimsing *et al*. 2009).

Lou *et al*. (2016) reported interactions between allelochemicals and the microbial community affecting weed seed germination following cover crop residue incorporation into the soil. Qu *et al*. (2021) invasive species allelopathy may decrease plant growth and microbial activity. Scavo *et al*. (2019) showed the importance of agronomic, nutritional and ecological relevance in the soil system. In contrast, Mishra *et al.* (2013) reported beneficial role of microbial contributor in reducing the allelopathic effects of weeds. Zhang et al. (2019) showed soil microbial metabolic activity and carbon utilization in rhizosphere soil of rape seed (*Brassica napus* L.).

Many researchers isolated secondary metabolites and identified in the leachate, exudates, and extracts. An excellent review of literature on allelochemicals of *Imperata cylindrica* on microbial community has been published by Kato-Nogochi (2022). Greenhouse and field studies showed that *Imperata* cylindrica altered the microbial community in the rhizosphere soil and affected the growth of several crop plants. This type of research needs to be planned to establish any role of microbial community.

Allelochemicals - availability

A less attention has been made in the fact that the allelochemicals may be released as mixtures with other compounds (Wu *et al*. 2002). Soils may also influence the relative activity of allelochemicals in combinations. Because allelochemicals are generally exuded in mixtures of metabolites that often include other allelochemicals (Uren *et al*. 2001), preferential sorption of compounds onto the soil matrix could further alter availability.

The disappearance of allelochemicals was delayed when present in a multi-solute mixture from both soils. This slow disappearance of allelochemicals in a mixture could be due to the combined effect of preferential degradation, where compounds with a stable ring structure and without a 3-C (acrylic) side chain are less susceptible to degradation, and competitive sorption, where less hydrophobic molecules are displaced into soil solution (Tharayil *et al.* 2008).

The interaction of allelochemicals in the soil matrix remains as one of the least understood areas in the research on allelopathy (Tharayil *et al.* 2006). Most of the allelopathic interactions take place in the soil, where allelochemicals are exuded through roots (Bias *et al.* 2006) or are released during decomposition of plant litter (Bonanomi *et al.* 2006, Siqueira *et al.*, 1991). Thus, soil matrix forms the primary medium for the transport of allelochemicals from a donor to a receiver plant. During this transportation, the soil matrix is capable of altering the bioavailability of allelochemicals by various processes including sorption and chemical and microbial degradation (Dalton 1989, Tharayil *et al.* 2006, Ohno 2001). Because allelochemicals are secreted in quantities far less than needed to overwhelm the soil processes, at the field level, the soil matrix becomes the governing factor in the allelopathic activity. Thus, in many cases allelochemicals are not found in phytotoxic quantities under field conditions (Tharayil *et al.* 2008).

CLIMATE CHANGE

Climate change can disrupt food production and availability with current agricultural practices. Projected increases in temperature, changes in precipitation patterns, occurrence of extreme weather events and reductions in water availability may all result in reduced agricultural productivity (Raj *et al.* 2022). Climate change involves rising temperatures (Tubiello *et al.* 2007, Gillet *et al.* 2011) and altered precipitation patterns, leading to tribalities of summer droughts. Weeds are influenced by these altered abiotic conditions (Duke *et al.* 2009, Singer *et al.* 2013). Rising atmospheric CO_2 is likely to alter the competition between weeds and crops (Gray and Brady 2016). Thus, weed management will likely to be altered or challenged.

Bois *et al.* (2013) discussed the climatic change on biotic interactions of pants. Changes in temperature and precipitation will also affect the species phenology in ways that we do not understand. Peters et al. (2014) while reviewing the impacts of climate change on weeds in agriculture, indicated that changes in the species composition and new species introductions are favored under climate change. Thus, facilitate major ecological and agronomical implications. Climate change has significant impacts on the distribution of species and alters ecological processes that result from species interactions (Gomez-Ruiz and Lacher Jr, 2019). Duke *et al.* (2009) reported responses of insect pests, pathogens and invasive plant species to climate change in the forest areas of northern North America. Soil microbes alleviate allelopathy of invasive plants (Li *et al.* 2015).

Root exudates in rhizosphere interactions with plants have been studies over the years (Bias *et al.* 2006). The general expected higher atmospheric temperature and lower/altered precipitations would constitute environmental stresses affecting plant growth and development. In addition, the expected plant stresses may result in less or more production of allelochemicals in plant. The information on allelochemical production in plants under increased temperature or CO_2 or under altered precipitation is very limited.

Effects of increased atmospheric CO_2 on C_3 and C_4 weed species and crops have been established (Ziska and Bounce 1997, Ward *et al.* 2001). Rising atmospheric temperature on weed and crop growth and development have been reported over the years. Studies on the effects of higher temperature on allelopathic effects of weeds on crops are limited. This type of management practices would be altered under higher temperature or altered precipitation ranges. Teasdale *et al.* (2012) reported expression of allelopathy in the soil environment as soil concentration and activity of benzoxazinoid released by rye cover crop residue.

Chadha *et al.* (2019) showed that soil moisture regimes influenced growth, photosynthetic capacity, leaf biochemistry and reproductive capabilities of the invasive agronomic weed *Lactuca serriola*. Medina-Villar *et al.* (2020) reported that environmental stress under climate change reduces plant performance yet increases the allelopathic potential of an invasive shrub. The varying effects of temperature and photosynthetic photon flux density on the expression of allelopathy was demonstrated by growth analysis (Bhowmik and Doll 1983). Similar studies could be conducted to show any allelopathic activity as influenced by temperature variations, altered moisture conditions in the soil. Bajwa (2005) reported various effects of arbuscular mycorrhizae (AM) and effective microorganisms (EM) in various plant under allelopathic stress. Environmental stress such as rising temperature any influence plant growth enhancing or decreasing production of allelopathic compounds.

Altered precipitation leads to dry or wet conditions to soil and can influence the growth of plants. Mausbach (2022) demonstrated the effects of water stress on growth and fecundity of velvetleaf (*Abutilon theophrasti*). *Abutilon threophrasti* can survive equator larger than 50% FC continuous water-stress conditions, although with reduced leaf number, plant height, and growth index compared with 75% and 100% FC. And these factors may induce production of allelochemicals.

ALLELOCHEMICALS - CHALLENGES

We currently have numerous examples of allelopathic effects on weed suppression either by allelochemicals or by joint action of residue and its altered chemicals. Many crop residues or cover crop residues have been used in crop production. Today, we are still looking for other allelopathic plants or weed species. We have made significant advances in this direction over the last several decades. However, we still have a long way to go in terms of using allelochemicals or developing plant cultivars that would be used for complete weed management. This approach would be more challenging as we face rising atmospheric CO_2, temperature and altered precipitation.

Using allelochemicals for successful weed management may have limitations. Some of these in implementing natural products or allelochemicals for effective weed management include: (i) allelochemicals are present in very low concentration, (ii) compounds have generally short half-lives, (iii) narrow spectrum weed selectivity, and (v) may have high cost of production.

The environmental fate of allelochemicals is a complex issue that is affected by the donor and receiver target plant species, as well as soil and environmental variables that affect the fate and functions of the chemicals in the soil complex. Knowledge concerning the variation in these factors is essential to use the allelopathic relationship among plants in agroecosystems to promote weed management. Some of the research areas include:

- Identify allelopathic plant species
- Isolate and identify compounds in relation to mode of action
- Determine the stability of allelochemicals in soil
- Identify microbial role in allelopathic activity
- Production of allelochemicals as affected by temperature and CO_2 and PPFD
- Establish allelopathic activity in weed suppression or control in cropping system

Despite many challenges in implementing the allelopathic concept in weed management, there is tremendous scope for exploring allelopathy phenomena for successful weed management. The bioavailability of allelochemicals under field conditions must be established for its effective role in weed management. Continued research on these areas is important and we must invest our resources in exploring allelopathy as a complimentary component in successful weed management.

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