

Rice allelopathy: strategy for weed management

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Abstract: One of the challenges in rice production is weed management. While synthetic herbicides have traditionally been used to address this issue, their long-term use can have detrimental effects on both the agroecosystem and human health. An alternative method lies in leveraging allelochemicals naturally present in rice, which are powerful tools for biological weed management. These allelochemicals are released by various parts of rice such as roots, stems, leaves, and other parts, and consist of a diverse range of compounds that can interact with the environment, as putative allelochemicals, including phenolics, terpenoids, fatty acids, steroid, and others. These compounds can damage the biochemical and physiological processes in weed, effectively inhibiting their growth. Over several decades of allelopathy study, it has been known that several rice varieties have the potential to inhibit the growth of weed and genes related to rice allelopathy have been identified. These genes are associated with allelochemicals biosynthesis which has been proven to suppress weed. Understanding the mechanisms of action and biological processes involved in allelopathy not only improves the knowledge but also provides valuable metrics for developing environmentally friendly weed management strategies in rice production.

Keywords: Allelopathy, allelochemicals, rice germplasm, weed management.

Abbreviations: ABA_the abscisic acid, MDA_malondialdehyde, PAL_ phenylalanine ammonia lyase, ROS_reactive oxygen specific.

Introduction

Rice is the most widely consumed cereal as a staple food in the world, specifically in Asia, Africa, and South America. It is grown in more than 100 countries, and production reached 755,474 thousand tons in 2019 (FAO 2021). However, as the population increases, the demand for rice also increases, necessitating increased production while maintaining grain quality. The increase in rice production must consider ecosystem sustainability, without damaging the environment. Recently, rice farming systems are currently facing challenges and risks, including yield stagnation caused by climate change or cultivation systems (Horie 2019; Tanaka et al., 2015). Overcoming stagnation presents a formidable challenge for scientists and agricultural experts. Addressing these challenges is important to ensure a sustainable and reliable supply of rice to meet the growing needs of the world population.

Weed poses a significant challenge in rice production, capable of reducing yields by up to 60% in various cropping systems (Islam et al., 2021). While herbicide application has been the most relied-on method for weed control, the ecological risk associated with herbicides in rice cropping systems cannot be ignored. Herbicides contribute to land and water toxicity, alter microbial composition, and indirectly influence plants, animals, and human health (van Bruggen et al., 2018). Therefore, there is a need for sustainable weed management, both in terms of plants, water, and the environment. Weed management using allelopathy is the most important consideration in securing food supply, whereby yield improves without increasing cost and causing environmental harm. Allelopathy is the ability of plants to stimulate or inhibit other plants' growth by chemical compounds, which can be beneficial, as well as harm other plants.

The concept of allelopathy is concerned with the release of chemical compounds into the environment, known as allelochemicals. These compounds are secondary metabolites of plants and microorganisms (bacteria, viruses, fungi) that influence processes in agroecosystems (Barazani and Friedman 2001; Li et al., 2017; Cheng et al., 2022). The secondary metabolites of plants are released by several processes, i.e., volatilization, leaching, decomposition, and root exudation (Stashenko et al., 2009; Ubersfeld et al., 2018; Xuan et al., 2005; Hao et al., 2010) and affect the adjacent plants or microorganisms. The ecologically relevant mechanism of allelopathy in the field, the chemical compounds in the soil must be at phytotoxic levels to influence the growth of target plants (Choesin and Boerner 1991). Furthermore, plant allelopathy is a complex biological process in the rhizosphere, influenced by many factors. Variations in the potential of plant allelopathy affect other plant stems, which is due to differences in allelopathy genes in the biosynthesis of allelochemicals, and

interactions between plants, soil, and microorganisms (Fang et al., 2015; Zhang et al., 2018; Lalljee and Facknath 2000; Li et al., 2020).

Rice is a crop widely used for allelopathy potential, effectively inhibiting weed across laboratory, greenhouse, and field settings (Khanh et al., 2009; Ma et al., 2014; Ho et al., 2020). Rice allelopathy is a tool to solve weed infestation in sustainable production. Previous studies focused on various aspects of rice allelopathy, including screening methods, isolation and identification of allelochemicals, and gene mapping. This review aims to underscore the potential of rice allelopathy to suppress weed, rice allelochemicals, gene mapping to breeding programs, and avenues for further investigation in rice allelopathy.

Potential rice allelopathy inhibit weeds

Numerous studies investigated the efficacy of rice allelopathy in suppressing weed growth, showing differences in allelopathy ability among different rice varieties. Various parts of rice known to be used as allelopathy are straw, husks, and roots. Some varieties inhibit weed growth, as indicated by a decrease in root and shoot length, and dry weight of weed (Dilday et al., 1998; Chung et al., 2001; Ghahari and Miransari 2009; Rahaman et al., 2021). Table 1 shows rice germplasms and commercial varieties known for their allelopathy potential ability against weed. The difference in variants in rice cultivars might be rice allelopathy is polygenetically (Ebana et al., 2001). On the other hand, differences in rice allelopathy also influence screening methods, and the identification of crop allelopathy potential can be used in laboratory, greenhouse, and field bioassay (Wu et al., 2001). A previous study by Khanh et al. (2009) reported that the inhibition of rice against barnyardgrass was lower in laboratory and greenhouse settings compared to field conditions, with rates ranging from 15% to 20% [18]. Laboratory screening serves as a valuable initial step in assessing allelopathy potential, followed by validation in greenhouse and field settings.

Identification of rice allelochemicals

Rice contains allelochemicals, secondary metabolites that significantly impact allelopathy by influencing plant physiology and growth regulation. Fig 1 shows that allelochemicals produced by rice serve as a defense response against induced weed (Kato-Noguchi et al., 2010). The release of allelochemicals by rice will affect weed growth. However, the secretion of allelochemicals in rice is a long process and influenced by many factors, including plants, climatic, and soil conditions. The effect of allelochemicals on weed can inhibit nutrient absorption, which ultimately suppresses weed growth, both roots and shoots.

Table 2 shows a comprehensive list of allelochemicals identified in rice, which are present in root exudates, straw, husk, or decomposing residue. These include phenolic compounds, momilactone, fatty acids, and some other chemical classes (Kato-Noguchi et al., 2002; Ko et al., 2005; Kong et al., 2004; Patni et al., 2019; Li et al., 2022). Therefore, allelochemicals identification of rice is important to know the modes of action of rice allelopathy (Table 3). All rice cultivars are capable of releasing momilactone compounds, with momilactone B exhibiting a more dominant inhibitory effect on the growth of weed compared to momilactone A (Kato-Noguchi et al., 2010). According to Quan et al., (2019), momilactone B has the strongest suppressive effect on weed, followed by momilactone A and combination of momilactone A and B (Quan et al., 2019). Momilactone B suppresses the germination and growth of *Arabidopsis* by disrupting ABA and auxin biosynthesis signaling pathways, consequently reducing auxin production and impairing the maintenance of root apical meristem (Wu et al., 2020). Furthermore, momilactone B inhibits the accumulation of several proteins (serine protease, amylin synthase LUP2, β -glucosidase, and malate synthase), which are important for the growth and development of *Arabidopsis* (Kato-Noguchi and Kitajima 2015) at concentrations >30 and $10 \mu\text{mol L}^{-1}$ (Kato-Noguchi et al., 2013).

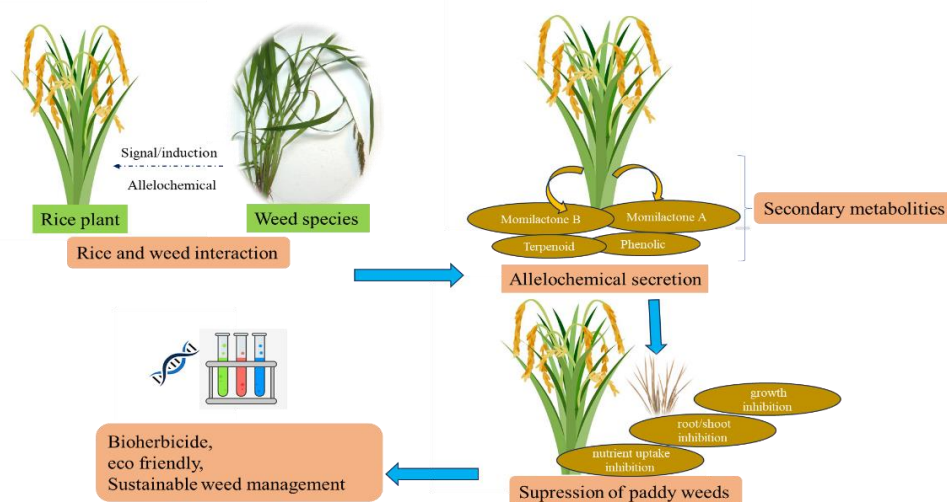
Some phenolic acids have a strong allelopathy effect on weed growth, although allelopathy activity depends on phenolic acid and the dose. Šćepanović et al., (2022) showed that phenolic acids (ferulic, *p*-hydroxybenzoic, vanillic, *p*-coumaric acid) inhibited the germination and growth of *Ambrosia artemisiifolia* L. when administered at higher doses than in plant tissues (Šćepanović et al., 2022). The inhibition of seed germination by phenolic compounds is attributed to their interference with amylase and gibberellin, subsequently altering reserve mobilization during embryo development. The lower doses of allelochemicals support the cellular antioxidant system by increasing the activity of enzymes to regain redox homeostasis (Đorđević et al., 2022). Understanding the dosage of allelochemicals released is crucial for determining their impact on the growth of surrounding plants. Moreover, mixed phenolic acid can significantly increase H_2O_2 , O_2^- , and MDA contents, suggesting a higher level of ROS and lipid peroxidation, which causes the cell membrane to be disrupted and cell homeostasis to be disturbed (He et al., 2022).

Genetic of rice allelopathy

Understanding the biosynthesis mechanism of allelochemicals in rice is closely associated with genetic regulation, an important aspect to comprehend. Commonly, the relationship between allelochemicals and their effect on other plants in the field is complex and influenced by changing environmental factors. However, a few studies showed gene regulation of a biological response, and the regulation of gene expression played an important role in the formation of rice allelopathy. Momilactones (A and B), isolated from hulls of rice are diterpenoid metabolites, known for their potential to inhibit the growth of other plants and defense against pathogens. Rice chromosome 4 consists of a dehydrogenase gene (AK103462), P-450 genes (CYP99A2 and CYP99A3), and two diterpene cyclase genes (OsCyc1 and OsKS4), plant gene contain biosynthetic gene cluster for momilactone biosynthesis (Shimura et al., 2007; Zhang and Peters 2020). Moreover, 14 genes were found to be upregulated, which are related to phenolic acid biosynthesis through real-time fluorescence quantitative PCR (qRT-PCR) methods. These genes are categorized into 5 groups, including signal transduction, growth-mediated

Table 1. Rice germplasms/cultivars with an allelopathy activity.

Germplasm/cultivars	Species	Screening	References
Lubang Red, YHI, Musashikogane, Taichung Native 1, Kouketsumuchi, Takanenishiki, AC1423, Tan Gang	<i>Echinochloa crus-galli</i>	Laboratory, field	Olofsdotter 2001
PI 312777, PI 338046, Lemont, Rexmont	<i>Heteranthera limosa</i> , <i>Ammannia coccinea</i> , <i>Echinochloa crus-galli</i>	Field	Dilday et al., 2001
Janganbyeon, Baekambyeon, Labelle Ilpum	<i>Echinochloa crus-galli</i>	Laboratory	Chung et al., 2002
Buldo, Agudo	<i>Echinochloa crus-galli</i>	Laboratory	Ko et al., 2005
Dinorado, Neda, Domsorkh, Dular	<i>Echinochloa crus-galli</i>	Field	Ahn et al., 2005
PI312777, Huagan-1, Huajianxian	<i>Echinochloa crus-galli</i> , <i>Cyperus difformis</i> , <i>Eclipta prostrata</i>	Laboratory, Greenhouse, field	Berendji et al., 2005 Kong et al., 2008
YI, U17, Nep Thom, Lua Huong, Nhi Uu, Khau Van, Phuc Tien	<i>Echinochloa crus-galli</i>	Laboratory, greenhouse, field	Khanh et al., 2009
Hinohikari, Nipponbare, Sasanishiki, Yukihihikari, Norin 8, Kamenoo, Koshihikari	<i>Lactuca sativa</i>	Laboratory	Kato-Noguchi et al., 2010
BR23, BR21, BR25, BR11, BR-5331-93-2-8-4, BR-5620-9-1-2, Lalparija, BR-5615-9-1-2, BRRI dhan 27	<i>Lactuca sativa</i> , <i>Echinochloa crus-galli</i>	Laboratory, greenhouse	Karim et al., 2012
Ld365	<i>Echinochloa crus-galli</i>	Field	Ranagalage et al., 2014
Koshihikari, Jasmine	<i>Lactuca sativa</i> , <i>Raphanus sativus</i> , <i>Echinochloa crus-galli</i>	Laboratory	Khanh et al., 2018
WITA 3, WITA 4, WITA 12, Fukuhibiki, Woo-Co, Kalizira	<i>Echinochloa crus-galli</i> , <i>Cyperus difformis</i> , <i>Cyperus iria</i> , <i>Fimbristylis milliacea</i> , weedy rice	Laboratory	Alam et al., 2018
OM 2395, OM 3536, OM 4498, OM 5930, OM 6976, OM 7347, OM N406, OM 380	<i>Echinochloa crus-galli</i>	Laboratory	Ho et al., 2020
Inpara 3, Inpara 4, Inpara 7, Inpara 9, Inpara 10	<i>Echinochloa crus-galli</i> , <i>Monochoria vaginalis</i>	Greenhouse	Sujinah et al., 2021

**Fig 1.** The process of rice allelopathy in suppressing weed.

transcription regulation, secondary metabolism, cell defense, protein synthesis, and degradation (Elshamey 2018). Genes related to rice allelopathy, phenolic acids, fatty acids, and flavonoids, which constitute the metabolites of shikimic acid and acetic acid pathways were classified into 3 categories, including biological process, the cellular component, and molecular function were found in rice allelopathy accession PI312777 through RNA sequencing (Zhang et al., 2019). Gene such as OsCPS4 (copalyl diphosphate synthase 4) and OsKSL4 (kaurene synthase-like 4) play direct role in the momilactones in

Table 2. Allelochemicals of rice.

Allelochemicals	Sources	References
Momilactone B	Root exudates	Kato-Noguchi et al., 2002
Momilactone A	Root, straw	Kato-Noguchi et al., 2008
Momilactone A, B	Straw	Lee et al., 1999
Momilactone A, B	Husk	Minh et al., 2018
Salicylic acid	Straw	Chung et al., 2001
p-coumaric acid		
o-hydroxyphenylacetic acid		
Syringic acid		
Ferulic acid		
Benzoic acid		
p-hydroxybenzoic acid		
m-coumaric acid		
o-coumaric acid		
3-isopropyl-5-acetoxycyclohexene-2-one-1	Root, straw, root	Kong et al., 2004
Momilactone B	exudates	
5,7,4 <i>o</i> -trihydroxy-3 <i>o</i> ,5 <i>o</i> -dimethoxyflavone		
2,4-dihydroxybenzaldehyde	Root, straw	Ho et al., 2020
2,6-dimethoxybenzoic acid		
3,4-dihydroxybenzoic acid		
3,4-dihydroxyphenylacetic acid		
3-hydroxybenzoic acid		
4-hydroxybenzoic acid		
5-methoxysalicylic acid		
7-oxostigmasterol		
Benzoic acid		
2,4-dimethoxybenzoic acid		
2,5-dihydroxybenzoic acid		
3,4-dimethoxybenzoic acid		
3,5-dihydroxybenzoic acid		
3,5-dimethoxybenzoic acid		
Cinnamic acid		
Coumarin		
Ergosterol peroxide		
p-hydroxycinnamic acid		
Salicylic acid		
Vanillic acid		
Fatty acids	Straw	Sujinah et al., 2021
Steroids		

Table 3. Mode of action of rice allelochemicals.

Allelochemical	Mode of action	Target	References
Ferulic Acid	Inhibits photosynthesis; reduces stomatal conductance	Several crops	Einhellig 1996
Crude extracts of allelopathic rice cultivars	Inhibit superoxide dismutase and catalase activities	Banyard grass seedling	Lin et al., 2000
Momilactones A, B, 1-tetratriacontanol	Inhibit chlorophyll content	Duckweed	Macias et al., 2005
Momilactone B	Inhibits accumulation of subtilisin-like serine protease, amryn sunthase LUP2, β -glucoside, malate synthase, breakdown of cruciferin 2	Arabidopsis thaliana	Quan et al., 2019

diterpene synthase (Xu et al., 2012), while OsPAL (phenylalanine ammonia lyase), OsC4H (cinnamate 4-hydroxylase), OsMOT (*O*-methyltransferase), and OsCAD (cinnamoyl-CoA) regulate the phenylpropanoid pathway, which is shown by the increased content of L-phenylalanine in rice allelopathy (Fang et al., 2020).

Advances of technologies in genomic sequencing affect crop improvement, include rice allelopathy. Use of RNA-seq to determine allelopathic response, have been identified 5684 DEGs (differentially expressed genes) and 388 genes were transcription factors. DEGs are genes associated momilactone and phenolic acids biosynthesis (Sultana et al., 2023). Zhang et al. (2019) classify DEGs into three categories, i.e the biological process, the cellular component, and the molecular

function. Moreover, the KEGG pathway show that the most genes include in various pathways, and phenylpropanoid biosynthesis play in controlling rice and barnyardgrass interaction (Sultana et al, 2023). The steps of phenylpropanoid derived synthesis are catalyzed by phenylalanine ammonia lyase (PAL), cinnamate-4 hydroxylase (C4H), and *p*-coumaroyl coenzyme A ligase (4CL). PAL facilitates to produce trans-cinnamic acid, a crucial precursor for phenolic compounds (García-Romeral et al., 2024). Therefore, the increase of secondary metabolites can serve as a target for selective molecular breeding or metabolic engineering for rice allelopathy to control weed and may also provide the improvement of rice allelopathy with more options by genetic modification.

Future study for rice allelopathy

Rice allelopathy is a long-term solution for weed management in paddy fields. While rice with weed-suppressing potential may not entirely replace chemical herbicides, it can still decrease their usage, leading to reduced production costs and increased profits for farmers. The evidence shows that rice allelopathy serves as a functional solution to ecological problems and contributes to sustainable agriculture through various means such as rice residues, rotation, or bioherbicides. Therefore, the following subjects are proposed for further investigation:

Investigating methods to increase allelochemicals content. Currently, the content of allelochemicals in rice is still relatively low necessitating an increase to enhance the efficacy in weed suppression.

Studies on combining rice with other plants for the development of bioherbicides are important. Many plants contain allelochemicals with the potential to inhibit the growth of other plants, making them promising candidates for bioherbicide formulation.

Determining the optimal amount of rice residue required for effective weed suppression is essential. Additionally, assessing whether the use of residues might lead to increased greenhouse gas emissions is important. Rice residues can serve as a food supply for methanogenic bacteria, which produce methane, potentially impacting greenhouse gas levels.

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