

Allelopathy of Barnyardgrass (*Echinochloa crus-galli*) Weed: an Allelopathic Interaction with Rice (*Oryza sativa*)

Tran Dang Khanh¹, Khat Huu Trung¹, La Hoang Anh¹, and Tran Dang Xuan²

¹ Department of Genetic Engineering, Agricultural Genetics Institute, Km2 Pham Van Dong Road, North Tu Liem, Hanoi 123000, Vietnam

² Graduate School for International Development and Cooperation (IDEC), Hiroshima University, Higashi-Hiroshima 739-8529, Japan

Abstract

Barnyardgrass (*Echinochloa crus-galli*) is one of the most pernicious and problematic weeds in worldwide agriculture. The objective of this review is to highlight the morphology and habitats of this weed, and to present comprehensive information of the allelochemical constituents and pharmacological effects as well as its allelopathic interaction with rice (*Oryza sativa* L.) based on 115 worldwide literary resources reported over the last 40 years. In laboratory bioassays and root exudates experiments, barnyardgrass showed remarkable inhibition on the growth of the indicator plants. In greenhouse and field experiments, depending on the proportion density of barnyardgrass interference, rice yield is significantly reduced. Major isolated chemical constituents [including 59 compounds, belonging to phenolics, terpenes, steroids, lactones, long-fatty acids, and their derivatives] were identified and isolated from the different parts of this weed including root exudates and infested-soil, which are involved in allelopathic action. Among these, *p*-hydroxymandelic acids, diethyl phthalate, and two lactones [7,8-dihydro-5,6-dehydrokavain (DDK) and 7,8-dihydrokavain (DHK)], along with a gene cluster for the biosynthesis of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), may be responsible for the inhibitory effects of barnyardgrass in paddy fields. In attempts to elucidate the modes of action of these allelochemicals and allelopathic interactions between rice and barnyardgrass, it has been shown that the allelopathic actions of barnyardgrass and rice have similar responses in that they sense allelochemicals in the exudation of roots for enhancing allelopathic activity. However, the questions of which compounds play a main role in barnyardgrass allelopathy, and the actual modes of allelopathic interactions with rice remain unclear. This review may provide new insights into barnyardgrass' adaptation and invasiveness as well as how the attributable interactions of all its

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Correspondence to
tdkhanh@vaas.vn

ORCID
Tran Dang Khanh
<https://orcid.org/0000-0003-4426-7121>
Xuan Tran Dang
<https://orcid.org/0000-0001-7103-5698>

present allelochemicals inhibit the growth of rice and the adjacent plants by allelochemical pathways.

Keywords

Allelopathy, allelochemical, interaction, barnyardgrass, *Echinochloa crus-galli*, root exudates, rice

Introduction

Barnyardgrass (*Echinochloa crus-galli*) belongs to the genus *Echinochloa* with over 250 plant species around the world, many of which are considered as noxious weeds. Barnyardgrass is native to Europe and has dispersed to many large areas around the world with diverse living environments including Asia, Australia, and America. It is one of the most important warm-season annual grass weeds. “*Crus*” is Latin for leg or shank, and “*galli*”, the possessive form of *gallus*, refers to cockspurs which is part of many of the plant’s later English common names (Mit, 1990). Some common names of *E. crus-galli* include watergrass, junglerice, cock's foot, cockspurgrass, barngrass, and barnyard millet (Mit, 1990). Barnyardgrass is one of the world’s worse rice weeds and causes problems in at least 61 countries and in over 36 different crops (Holm *et al.*, 1991) due to its superior biology and tremendous ecological adaptations. It has strong allelopathic potential and is widely used as an indicator plant in allelopathic research (Dilday *et al.*, 2001; Khanh *et al.*, 2007a; Khanh *et al.*, 2007b; Khanh *et al.*, 2018; Ranagalage *et al.*, 2015).

In paddy fields, barnyardgrass competes with rice (*Oryza sativa* L.) for environmental factors such as light, water, space, nutrition, and other resources. In addition, the C₄ pathway of carbon fixation helps barnyardgrass to out-compete C₃ rice plants (Vidotto *et al.*, 2007), causing a significant reduction in rice yield up to 85% (Nguyen, 2015). Specifically, competition from 25 barnyardgrass plants m⁻² can cause a 50% reduction in rice yield (Chin, 2001). Barnyardgrass competing with dry-seeded rice can reduce rice yield from 8 to 79% beginning at crop emergence and lasting for

periods ranging from 15 days to maturity (Malik *et al.*, 2003). Specifically, one barnyardgrass plant spaced 40 cm from a rice plant reduces the rice yield by 27% (Stauber *et al.*, 1991). Rice tiller number was significantly decreased with an increasing population of barnyardgrass (Mennan *et al.*, 2012). Weed infestation with high density can absorb 60 - 80% of the nitrogen available to the crop and affects crop growth negatively (Wilson *et al.*, 2014).

In direct-seeded rice in the Mekong delta, the species *E. crus-galli* is dominant at more than 50% of the 197 sites surveyed and common at over 35% of the remaining sites (Chin *et al.*, 1998), where japonica varieties showed a greater yield loss comparing with indica hybrids (Zhang *et al.*, 2017a). The losses of rice yield due to barnyardgrass competition across the globe are estimated at about 35% (Oerke and Dehne, 2004). Other studies have shown that barnyardgrass removes 60 - 80% of the available nitrogen from the soil and hosts the viruses that produce tungro and dwarf disease in rice (Holm *et al.*, 1991; Allen *et al.*, 1995). Several recent reports have documented the competition between barnyardgrass and food crops by focusing on competition duration, time of emergence, weed density, and crop sowing method which all have significant influence on the magnitude of competition and yield losses (Ottis and Talbert, 2007; Bajwa *et al.*, 2015; Chauhan, 2013; Chauhan and Abugho, 2012). Barnyardgrass has great persistency, grows profusely, synchronizes growth requirements with rice, and reduces the growth of various components of rice (Fischer *et al.*, 1997). This weed also causes changes in the quality of rice including kernel, chalky size, and gel consistency which were remarkably lower as compared with the control due to the interference in canopy light transmission caused by barnyardgrass (Zhang *et al.*, 2017a). Moreover, some recent studies have reported that the leaf photosynthetic rate of barnyardgrass directly influenced the biomass and yield of rice (Baig *et al.*, 2005; Zhang *et al.*, 2009; Yamori *et al.*, 2016). This weed is being considered as one of the most dangerous herbicide resistant weeds of the world. Nguyen (2015) reported that 34 out of 65 barnyardgrass

populations collected in Australia were resistant to glyphosate with increasing resistant levels by 2 to 11-fold and evolved resistance to three acetolactate synthase enzymes in rice in Arkansas (Norsworthy *et al.*, 2014). Various biotypes of barnyardgrass have reported resistant to a variety of herbicides (Wilson *et al.*, 2014). This weed has evolved both target-site and non-target-site herbicide resistance, making it among the most noxious herbicide resistant weeds of the world (Bajwa *et al.*, 2015; Norsworthy *et al.*, 2014).

The objectives of this review are: (1) to highlight morphology, habitats, and economic importance of barnyardgrass; (2) to provide an insight of the allelopathic research of this weed, as well as (3) the interaction between barnyardgrass and rice via allopathic pathways; and (4) to indicate further work needed within the allelopathy of barnyardgrass and rice research.

Morphology and Habitats

E. crus-galli (barnyardgrass) consists of three phases (embryonic, vegetative, and reproductive) in its growth and development. Barnyardgrass plants are self-compatible and highly autogamous. It grows well in wet, muddy, warm, and rich soils. Individual barnyardgrass plants were reported to produce from 30,000 to over 200,000 seeds, with an average of 100,000 seeds per plant, depending upon environmental conditions (Norris, 1992). Under ideal conditions, one million seeds can be produced per plant (Gibson *et al.*, 2002). They may remain 90% viable for up to 3 years in the field and dormant for 8 - 9 years, during which germination is usually staggered (Hitchcock, 1971; Chin, 2001). Germination in barnyardgrass is hypogeal; the mesocotyl elongates, pushes the coleoptile toward the soil, and the plumule is enclosed in coleoptiles (Maun and Barret, 1986). Barnyardgrass seeds can germinate at a soil pH range of 4.0 - 8.0. This weed can survive and develop in areas with temperatures from 6 - 28°C, and is highly adapted to a wide range of photoperiods. The optimal conditions for seed germination are 30 - 37°C (McGillion and Storrie, 2006). For

seedlings, they grow best at 30°C, are sluggish at 10°C, and stopped growing at 5°C. Barnyardgrass grows best in warm muddy soil with a high nitrogen content and plenty of sunlight. Even with the dramatic impacts of climate change, barnyardgrass as a C₄, short day, annual, and tropical weed, has a tendency to grow better under harsh climates (Rao *et al.*, 2007; Juliano *et al.*, 2010; Bajwa *et al.*, 2015). It is also capable of competing well with C₃ crop plants such as rice, as it is able to out-compete C₃ plants under conditions of higher temperatures and limited water availability, scenarios projected to be caused by climate change (Rodenburg *et al.*, 2011). The average seed weight of *Echinochloa crus-galli* is 1.7 - 2.1 mg. Over 50% of the seeds produced are spread in irrigation water within 4 - 5 days and delivered to other sites. The seeds were reported as 100% viable after 6 to 8 years in storage, and after being properly germinated were grown for long periods of time in a completely O₂-free environment, which may contribute to the plant's ability to emerge from submerged conditions (Rumpho and Kennedy, 1981; Wilson, 1979). Yamasue *et al.* (1989) demonstrated that two epistatic genes were responsible for anaerobic germination in *Echinochloa* species, which may depend on sequential processes for regulation at the germination level.

Anaerobic metabolism in *Echinochloa* proceeds primarily via glycolysis, with partial operation of the tricarboxylic acid cycle and negligible to no oxidative phosphorylation (Kennedy *et al.*, 1983). However, under flood conditions with 10 cm of water, the seeds may be halted (Yabuno, 1983), but if the plant is already established, flooding does not hinder growth (Allen *et al.*, 1995). During winter, barnyardgrass survives as seeds on or under the soil surface then commonly germinates in late spring after the soil has warmed. Some seeds continue to germinate over the summer. It completes its life cycle during the summer and declines annually after seed production in September and October. In terms of propagation, *Echinochloa* spp. mainly reproduce sexually, although stem nodes can root when stems lie prostrate on the ground allowing



Figure 1. Barnyardgrass (*Echinochloa crus-galli*) (Feedipedia, 2018)

asexual reproduction under some circumstances (Holm *et al.*, 1991). Mujer *et al.* (1993) reported that among six *Echinochloa* species, four species, namely *E. phyllopogon* (Stev.) Koss, *E. muricata* (Beauv.) Fern, *E. oryzoides* (Ard) Fritsch Clayton, and *E. crus-galli*, are tolerant of anaerobiosis and germinate in the absence of oxygen. In bioassay tests, rice and barnyardgrass were able to germinate and grow under a strict nitrogen atmosphere (Kennedy *et al.*, 1990). A main difference between rice and barnyardgrass in their response to adding KCN was that rice germination was uninfluenced by KCN but suppressed by SHAM (apparently switching to a SHAM-sensitive pathway), while germination of barnyardgrass was inhibited by KCN with or without SHAM (Kennedy *et al.*, 1983). The identified enolase (2-phospho-D-glycerate hydrolase) and its activity in barnyardgrass were responsible for the anaerobic stress protein and was induced 5-fold in anoxically treated seedlings of three flood-tolerant *Echinochloa* species (*E. oryzoides*, *E. Phyllopogon*, and rice but was not in the flood-intolerant species (*E. crus-pavonis*) (Fox *et al.*, 1995).

Barnyardgrass has many growth characteristics that are similar to rice plants and it is difficult to distinguish between the two in the early stages of growth, causing farmers to

sometimes unknowingly transplant this weed into the field (Chauhan, 2013). Due to its mimicry with rice plants, barnyardgrass can easily escape manual weeding and can invade a wide range of soils and environments (Gibson *et al.*, 2002). It may have already led to a significant yield loss by the time it is recognized in the field (Khanh *et al.*, 2008; Bajwa *et al.*, 2015). The height of barnyardgrass can reach up to 1 - 2 m. Barnyardgrass reproduces annually with seeds produced via caryopsis; the ovary wall is fused with a seed coat, which is typical for many weeds (Koo *et al.*, 2000). The roots are fibrous in nature. The culm is smooth, free from hair, sturdy, and thick. It produces lateral branches and roots emerge from the decumbent base (Bajwa *et al.*, 2015). Seed heads are often purplish and consist of crowded spikelets with large seeds. The stem is stout and tufted. At the seedling stage, juvenile leaves are rolled and smooth, while a fully developed leaf may have smooth or scabrous margins (Maun and Barret, 1986). The leaves are flat, linear, and lanceolate up to 40 cm long and 5 - 15 mm wide. Ligules are absent. The barnyardgrass inflorescence is a green-to-purple apical panicle of 5 - 40 spike-like racemes. Culms are erect and ascending with wide phenotypic variation. The flowers are panicles; large numbers of small-sized flowers are attached to rachis through tiny stalks (Chin, 2001).

Spikelets are elliptical and pointed, 3 - 4 mm long, commonly green or reddish-purple with bristles on outer scales, and awned or awnless with wide variations. The panicle is 8 - 25 cm in length and has densely flowered spreading branches. Barnyardgrass flowers yearly and propagates by seeds. Barnyardgrass can most easily be distinguished from other grasses by its seedhead and the fact that it has no ligule (Khanh *et al.*, 2008; Bajwa *et al.*, 2015).

Economic Importance

The seeds of barnyardgrass are grown as fodder for livestock and as millet for human consumption in many tropical African and Asian countries (Hitchcock, 1971; Molla *et al.*, 2016). It is traditionally used to reduce body weight, lower blood sugar, treat hypertension, and help detoxify the liver and kidneys (Duke and Wain, 1981). Portions of the fresh plant are also used for treating carbuncles, haemorrhaging, sores, spleen trouble, wounds, and cancer (Mannetje and Jones, 1992; Molla *et al.*, 2016). Barnyardgrass is occasionally considered a “wonder grass” or “billion-dollar grass” and was recommended for forage as green feed, silage, or hay. However, it proved too succulent for hay and its use declined with the introduction of other high producing crops of greater value (Maun and Barrett, 1986). Nevertheless, barnyardgrass has been used for nourishing sheep as part of Australia’s drought mitigation program. Recently, barnyardgrass seeds are commonly used as target species (indicator plant) to evaluate the allelopathic ability of plants because barnyardgrass displays strong allelopathic activities and has weed suppression potential via allelopathy with higher plants (Khanh *et al.*, 2007a; Khanh *et al.*, 2007b).

Biological Activity

Recent reports demonstrated that barnyardgrass has several pharmacological effects including antidiabetic, anticancer, antioxidant, antimicrobial, hypolipidemic and anti-obesity activities. Specifically, extracts of barnyardgrass grains showed high *in vivo* antidiabetic and antioxidant activities, of which,

a 70% hydroalcoholic extract showed significant antidiabetic activity in normal and alloxan induced diabetic rats (Devi *et al.*, 2012; Ho *et al.*, 2012; Mehta and Vadia, 2014). Two novel defesins, Ec-AMP-D1 and EcAMP-D2, that differ by a single amino acid substitution were isolated by a combination of different chromatographic procedures. Those defesins were shown to be active against several phytopathogenic fungi and the oomycete *Phytophthora infestans* at micromolar concentrations (Odintsova *et al.*, 2008). Another novel lipid transfer protein (Ec-LTP) was isolated from the caryopsis of barnyardgrass, and contained eight cystein residues with four disulfide bonds that also remarkably suppressed the development of the pathogenic fungi *Phytophthora infestans* and *Helminthosporium sativum* which cause the late blight of potato and tomato, and the root rot of herbs, respectively (Rogozhin *et al.*, 2009). Also, the peptide EcAMP1 and polypeptide EcAMP3 were isolated from a crude acidic extract of barnyardgrass grains which revealed significant antifungal activity (Nolde *et al.*, 2011) and antibacterial activity *in vivo* (Ryazantsev *et al.*, 2013). A recent report of Molla *et al.* (2016) showed a high cytotoxic activity of a methanolic extract of barnyardgrass against four human cancer cells was found, of which two methoxylated flavonoids and one methoxylated cinnamic acid were shown to be the most active and may be considered as alternative compounds for the treatment of human cancers (Molla *et al.*, 2016). The hydroalcoholic extracts of barnyardgrass grains showed significant reductions in body weight, adipose tissue weight, and blood glucose levels of albino rats (Pavani *et al.*, 2014).

Allelopathic Research of Barnyardgrass

Allelopathy is considered to be a particular form of amensalism that causes a negative interaction in which one plant is inhibited while the other is unaffected. Stated another way, allelopathy is considered to be chemical interactions between plants that interfere with the growth of nearby plants, mediated by the release of plant-produced bioactive secondary

metabolites referred to as allelochemicals (Khanh *et al.*, 2018). Barnyardgrass is a noxious plant and considered an invasive weed, causing difficulties for many food crops around the world, especially rice. In recent years, allelopathy is often invoked as a potential mechanism of invasive plant impact and success (Hierro and Callaway, 2003; Inderjit *et al.*, 2008). Barnyardgrass has received much attention to examine its allelopathic potential as well as to identify its allelochemicals due to its invasiveness in nature.

Laboratory bioassays

Laboratory bioassays are useful and necessary for initial allelopathic examinations. Recently, Esmaeili *et al.* (2012) reported that an extract of mature barnyardgrass had a phytotoxic effect on rice genotypes with the ranking: leaf extract > hull extract > stem extract. An aqueous methanol extract of whole barnyardgrass plants (ripening stage) at 0.01 g dry weight showed a suppressive effect on root growth of rice and alfalfa by 19.8% and 43.7%, respectively, and inhibited the root growth of cress (*Lepidium sativum*), alfalfa (*Medicago sativa*), lettuce (*Lactuca sativa*), and rice by 15.0, 42.7, 3.7, and 46.6%, respectively. By increasing the extract concentration to greater than 0.1 g dry weight, all the tested plants were significantly inhibited and the extract

completely suppressed both shoot and root growth of lettuce (Figure 2) (Son *et al.*, 2010). The active fractions of a 1.0 g barnyardgrass extract partitioned by silica gel and sephadex columns (40% methanol) showed the most suppressing effect on the growth of shoots and roots of cress by 75.6 and 88.2%, respectively (Son *et al.*, 2010). In other studies, Jabran *et al.* (2010) and Esmaeili *et al.* (2012) showed that barnyardgrass aqueous extracts had phytotoxic effects on rice by significantly inhibiting the growth of *Avena fatua* L and *Phalaris minor* Retz, depending on the concentration of the barnyardgrass extracts. Recent reports revealed that extracts made from roots and aerial parts of barnyardgrass caused reduced germination and inhibited early seedling growth of rice and soybean (Chopra *et al.*, 2017).

Root exudates experiments

Our previous studies have shown that root exudates of young barnyardgrass plants exhibited significant inhibitory effects on the emergence of lettuce, rice, and monochoria (Khanh *et al.*, 2008). In a bioassay experiment, ten grams of healthy barnyardgrass were grown in glass pots with distilled water for 7 days in a growth chamber. The resulting root exudates were set as the original dose. The density of barnyardgrass at 50 - 100 seeds per Petri dish caused 30 - 40% inhibition on the germination

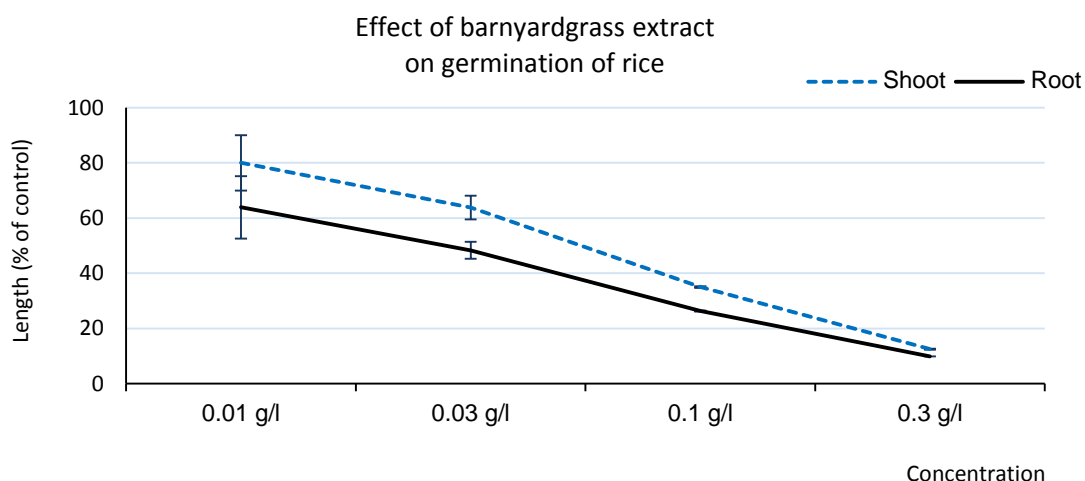


Figure 2. Inhibition of barnyardgrass extract on the growth of rice seedlings (Son *et al.*, 2010)

of rice. Germination of lettuce and monochoria was reduced at two applied doses in comparison with the controls. At the original full dose, lettuce emergence was suppressed by about 90%. However, at one-half dose, the roots of monochoria and rice were both inhibited by a similar level (about 30%), whereas lettuce roots were suppressed by about 45% (Xuan *et al.*, 2006). In another experiment, root exudates of young barnyardgrass plants (2 - 12 days old) revealed allelopathic effects and plant-selective activity, and inhibited shoot growth and root elongation of cockscomb, timothy, and cress (Yamamoto *et al.*, 1999). Also, a culture solution of barnyardgrass (2-month-old plants) revealed strong inhibition on the seedling growth of lettuce and mung bean at a 500 ppm concentration. However, the root exudates did not inhibit the shoot growth of barnyardgrass, which was similar with the report of Khanh *et al.* (2008). Additionally, a recent report showed that root exudates of barnyardgrass seedlings increased allelopathic activity when barnyardgrass was grown with rice (Kato-Noguchi, 2011). Barnyardgrass root exudates from hydroponics showed significant suppression of the growth of Dullar rice cultivar. The degree of inhibition of the barnyardgrass root exudates was enhanced by increasing its concentration (Heidarzade *et al.*, 2012).

Greenhouse and field trials

Pot experiments conducted in the greenhouses of the Cuulong Delta Rice Research Institute (CLRRI) demonstrated that dry biomass of barnyardgrass was indirectly proportional to the dry rice biomass and reduced rice yield. For instance, two, four, six, and eight plants of barnyardgrass plants were 123.0, 172.0, 168.0, and 262.0 g pot⁻¹, while rice biomass was 70.9, 48.6, and 34.3 g pot⁻¹ as compared with the weed-free control of 117.6 g pot⁻¹ (Chin, 2001). Rice yield was also decreased when grown with barnyardgrass. Trung *et al.* (1995) also reported that an infestation of less than 5 plants m⁻² of barnyardgrass in transplanted rice showed negligible effects on yield production. However, yield losses ranged from 7 to 13% when the

infestation rate increased to 5 - 10 plants m⁻² and losses increased again to 23 - 27% at an infestation rate of 15 - 35 plants m⁻². In wet-seeded rice during the summer-autumn season, populations of 7, 11, 99, and 258 barnyardgrass plants m⁻² (corresponding to dry weights of 64, 126, 233, and 484 g m⁻²) caused yield losses by 10.5, 15.8, 38.8, and 86.8%, respectively. While in the winter-spring season, 87, 254, and 340 plants m⁻² (corresponding to 188, 623, and 943 g m⁻²) reduced rice yield by 19.0, 50.0, and 63.5%, respectively. In paddy field screening, the density of 25 barnyardgrass plants m⁻² caused a 50% reduction in rice yield (Chin, 2001). Similarly, previous research of Smith Jr. (1974) reported that competition with barnyardgrass for 10 or 20 days did not reduce rice grain yield. However, barnyardgrass at density of 57 plants m⁻² reduced rice yield by 50%. Rice yield reduction may be variable because of the allelopathic ability of rice landraces, however, when rice competed with barnyardgrass for 40 days or longer, rice yield was significantly reduced (Khanh *et al.*, 2007b). On the other hand, rice yield losses have been found to be directly proportional with the present density of barnyardgrass weeds. In pot culture experiments, Leela *et al.* (2018) demonstrated that an aqueous extract of barnyardgrass showed significant inhibition in some vegetable crops, which implied that barnyardgrass is a strong allelopathic weed, causing trouble to a wide range of crops.

Barnyardgrass contains many major secondary metabolites in its aerial and root exudates. A total of 59 compounds have been identified and isolated from the leaves, stems, roots, root exudates, and infested-soil including phenolics, terpenes, steroids, lactones, long-fatty acids, and their derivatives which were involved in allelopathic action, of which phydroxymandelic acids, diethyl phthalate, and two lactones [7,8-dihydro-5,6-dehydrokavain (DDK) and 7,8-dihydrokavain (DHK)] and their derivatives (Table 1). Li *et al.* (1992) reported that two main allelochemical compounds, *p*-hydroxybenzaldehyde and *p*-hydroxybenzoic acids, and the vanillic acid 3,4-dihydroxybenzoic were identified in the cultural

Table 1. The allelochemicals identified and isolated from the barnyardgrass

No	Name of substance	Chemical classification	Source	References
1	2-Ethyl-phenol	Phenol	Root exudate	Xuan <i>et al.</i> (2006)
2	2,4-bis (1,1-Dimethyl)-phenol	Phenol	Root exudate	Xuan <i>et al.</i> (2006)
3	3,4-Dihydroxybenzoic	Phenol	Root exudate	Li <i>et al.</i> (1992)
4	Dimethyl ester-phthalic acid	Phthalic acid derivative	Root exudate	Xuan <i>et al.</i> (2006)
5	Butyl 8-methylnonyl ester-phthalic acid	Phthalic acid derivative	Root exudate	Xuan <i>et al.</i> (2006)
6	Diisooctyl ester-phthalic acid	Phthalic acid derivative	Root exudate	Xuan <i>et al.</i> (2006)
7	Diethyl phthalate	Phthalate ester	Root exudate	Xuan <i>et al.</i> (2006)
8	Ethyl ester-4-ethoxy-benzoic acid	Benzoic acid derivative	Root exudate	Xuan <i>et al.</i> (2006)
9	2,3,7-Trimethyl-decane	Decane derivative	Root exudate	Xuan <i>et al.</i> (2006)
10	2-Methyl-dodecane	Decane derivative	Root exudate	Xuan <i>et al.</i> (2006)
11	Acenaphthene	Polycyclic aromatic hydrocarbon	Root exudate	Xuan <i>et al.</i> (2006)
12	Decanoic acid	Long chain fatty acid	Root exudate	Xuan <i>et al.</i> (2006)
13	Myristic acid	Long chain fatty acid	Root exudate	Xuan <i>et al.</i> (2006)
14	Stearic acid	Long chain fatty acid	Root exudate	Xuan <i>et al.</i> (2006)
15	Pentadecanoic acid	Long chain fatty acid	Root exudate	Heidarzade <i>et al.</i> (2012)
16	7,8-Dihydro-5,6-dehydrokavain	Lactone	Root exudate	Xuan <i>et al.</i> (2006)
17	7,8-Dihydrokavain	Lactone	Root exudate	Xuan <i>et al.</i> (2006)
18	2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA)	Hydroxamic acid	Metabolic gene cluster	Guo <i>et al.</i> (2017)
19	Momilactone A	Momilactone	Metabolic gene cluster	Guo <i>et al.</i> (2017)
20	<i>p</i> -Hydroxybenzaldehyde acid	Phenolic acid	Root exudates	Li <i>et al.</i> (1992)
21	<i>p</i> -hydroxymandelic acid	Phenolic acid	Root exudate	Yamamoto <i>et al.</i> (1999)
22	<i>p</i> -hydroxybenzoic acid	Phenolic acid	Root exudates	Li <i>et al.</i> (1992); Heidarzade <i>et al.</i> (2012)
23	5,7-dihydroxy-3',4',5'-trimethoxy flavone	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
24	5,7,4'-trihydroxy-3',5'-dimethoxy flavone (tricin)	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
25	Flavone	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
26	Quercetin	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
27	Apigenin-8-C-sophoroside	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
28	Quercetin-3-O-glucoside	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
29	2-methoxy-4-hydroxy cinnamic acid	Phenolic acid	Grain	Molla <i>et al.</i> (2016)
30	Arbutin	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
31	Ferulic acid	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
32	Resorcinol	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
33	Salicylic acid	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
34	Caffeic acid	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
35	Vitexin	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
36	Umbelliferone	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
37	4-oxycoumarin	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
38	Robinin	Phenolic acid	Whole plant	Kumar <i>et al.</i> (2013)
39	Cinnamic acid	Phenolic acid		Heidarzade <i>et al.</i> (2012)
40	Linalool	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
41	<i>L</i> -Camphor	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
42	<i>Iso</i> -Borneol	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
43	4-Terpinenol	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
44	5-Isopropyl-2-methylbicyclo[3.1.0]hexan-2-ol	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
45	Coumaran	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
46	Methyl phenethyl ketone	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
47	Cinnamic aldehyde	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
48	Methyl ester cinnamic acid	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
49	1,5,5,8-Tetramethyl-12-oxabicyclo(9.1.0)-dodeca-3,7-diene	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
50	2-(4a,8-Dimethyl-1,2,3,4,4a,5,6,7-octahydro-2-naphthalenyl)-2-propanol	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
51	<i>p</i> -Hydroxy-methyl ester-cinnamic acid	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
52	Guaiol	Terpene	Infested soil	Khanh <i>et al.</i> (2008)
53	Methyl ester ferulic acid	Ferulic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
54	<i>m</i> -Hydroxy-methyl ester-cinnamic acid	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
55	2,4-Dimethoxycinnamic acid	Cinnamic acid derivative	Infested soil	Khanh <i>et al.</i> (2008)
56	Methyl pimar-7-en-18-oate	Steroid	Infested soil	Khanh <i>et al.</i> (2008)
57	Vanillic acid	Phenolic acid	Root exudate	Li <i>et al.</i> (1992)
58	<i>p</i> -coumaric acid	Phenolic acid	Root exudate	Esmaeili <i>et al.</i> (2012); Molla <i>et al.</i> (2016)
59	<i>m</i> -coumaric acid	Phenolic acid	Root exudate	Esmaeili <i>et al.</i> (2012)

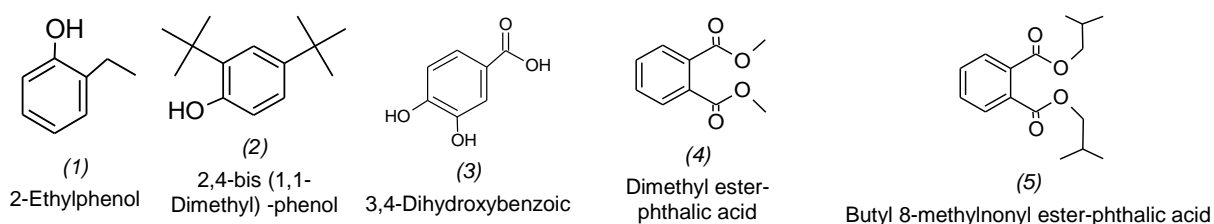
solution released by the roots of barnyardgrass using HPLC and ^1H NMR. Yamamoto *et al.* (1999) isolated and identified a potent allelochemical, p-hydroxymandelic acid, from the seeds of barnyardgrass growing in the vicinity of rice seedlings. This compound inhibited the growth of rice at the concentrations of 59.5 - 178.6 μM . In another experiment studying barnyardgrass root exudates collected from young barnyardgrass plants, 15 compounds potentially involved in the phytotoxic activity of barnyardgrass were identified. Of which, the quantities of diethyl phthalate, decanoic acid, myristic acid, stearic acid, 7,8-dihydro-5,6-dehydrokavain, and 7,8-dihydrokavain were 2.7, 11.1, 19.6, 35.5, 10.3, and 15.5 $\mu\text{g mL}^{-1}$ in the barnyardgrass root exudates, respectively. The two lactones revealed the greatest inhibition, followed by the phenolics, and then the derivatives of phthalic acids (Xuan *et al.*, 2006). The chemical structures of the 59 compounds are shown in Figure 3.

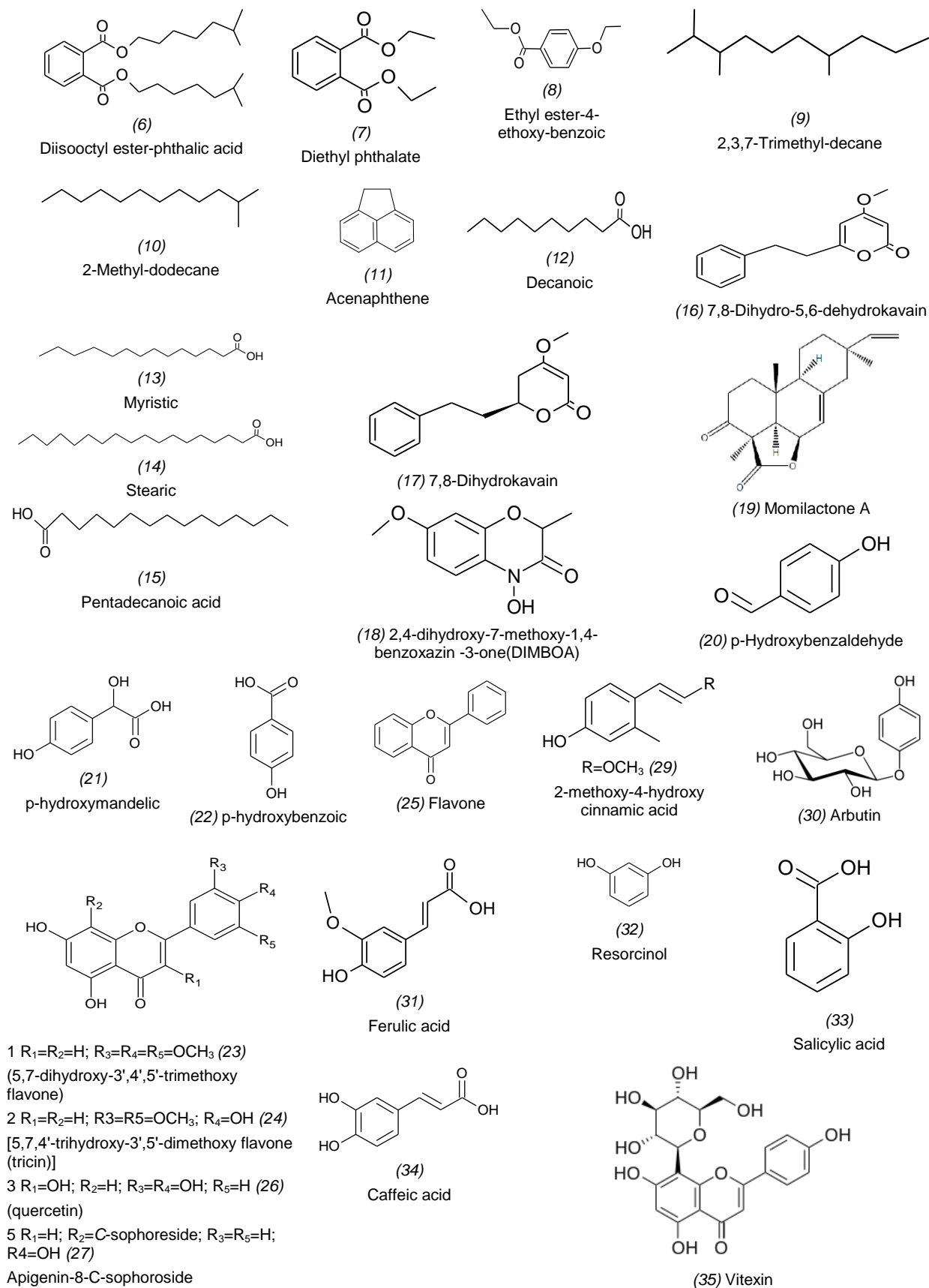
Allelochemicals identified in barnyardgrass

Heidarzade *et al.* (2012) used the HPLC method to qualify and quantify allelochemicals from barnyardgrass root exudates-hydroponics. The result showed that the highest content was p-hydroxybenzoic acid (4.3 mg L^{-1}) and the lowest was cinnamic acid (0.91 mg L^{-1}). Most of the isolated compounds from root exudates of barnyardgrass were identified as inhibitor substances which could be released into the environment and may contribute to the success of barnyardgrass as an invasive species (Xuan *et al.*, 2006). In another report, 18 compounds belonging to terpenes, derivatives of cinnamic acid and ferulic acid, long-chain fatty acids, and steroids were isolated and identified in soil samples from a barnyardgrass-infested field. GC-MS analysis showed that linalool, 4-

terpinenol, coumaran, methyl phenethyl ketone, and methyl ester cinnamic acid were in the samples at rates of 1.42, 0.37, 0.02, and 4.59 $\mu\text{g g}^{-1}$, respectively. The herbicidal activity varied among the isolated compounds. Specifically, methyl phenethyl ketone and methyl ester cinnamic acid showed stronger herbicidal effects than coumaran, linalool, and 4-terpineol (Table 1; Figure 3). Of note, the mixture of these compounds exhibited low suppression on the growth of barnyardgrass, but significantly inhibited the growth of other plants including rice and monochoria. The findings suggested that barnyardgrass possesses a potent phytotoxic substance and releases it into the soil to compete with rice and other paddy weeds in its vicinity by chemical pathway (Khanh *et al.*, 2006). Also, the possible involvement of chemical mediated interactions in allelopathy between rice and barnyardgrass when grown together may have generated the chemical cross talk that activated defense mechanisms against some biotic stress conditions by detection of certain key compounds (Kato-Noguchi and Ino, 2013).

The discovery of new metabolic pathways via plant genome sequencing has greatly accelerated recently. A secondary metabolic gene cluster was discovered to be self-contained cassettes for metabolite production (Osborn, 2010). Clustering of the genes controlling the biosynthesis of plant secondary metabolites, which were involved in allelopathic activities, was reported (Boycheva *et al.*, 2014). In barnyardgrass, a draft genome has been completed, and two gene clusters related to the biosynthesis of the allelochemical 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and the phytoalexin momilaton A were found in the genome of barnyardgrass (Guo *et al.*, 2007).





8 R₁=O-β-D-glucopyranoside; R₂=H;
R₃=R₄=OH; R₅=H (28)
Quercetin-3-O-glucoside

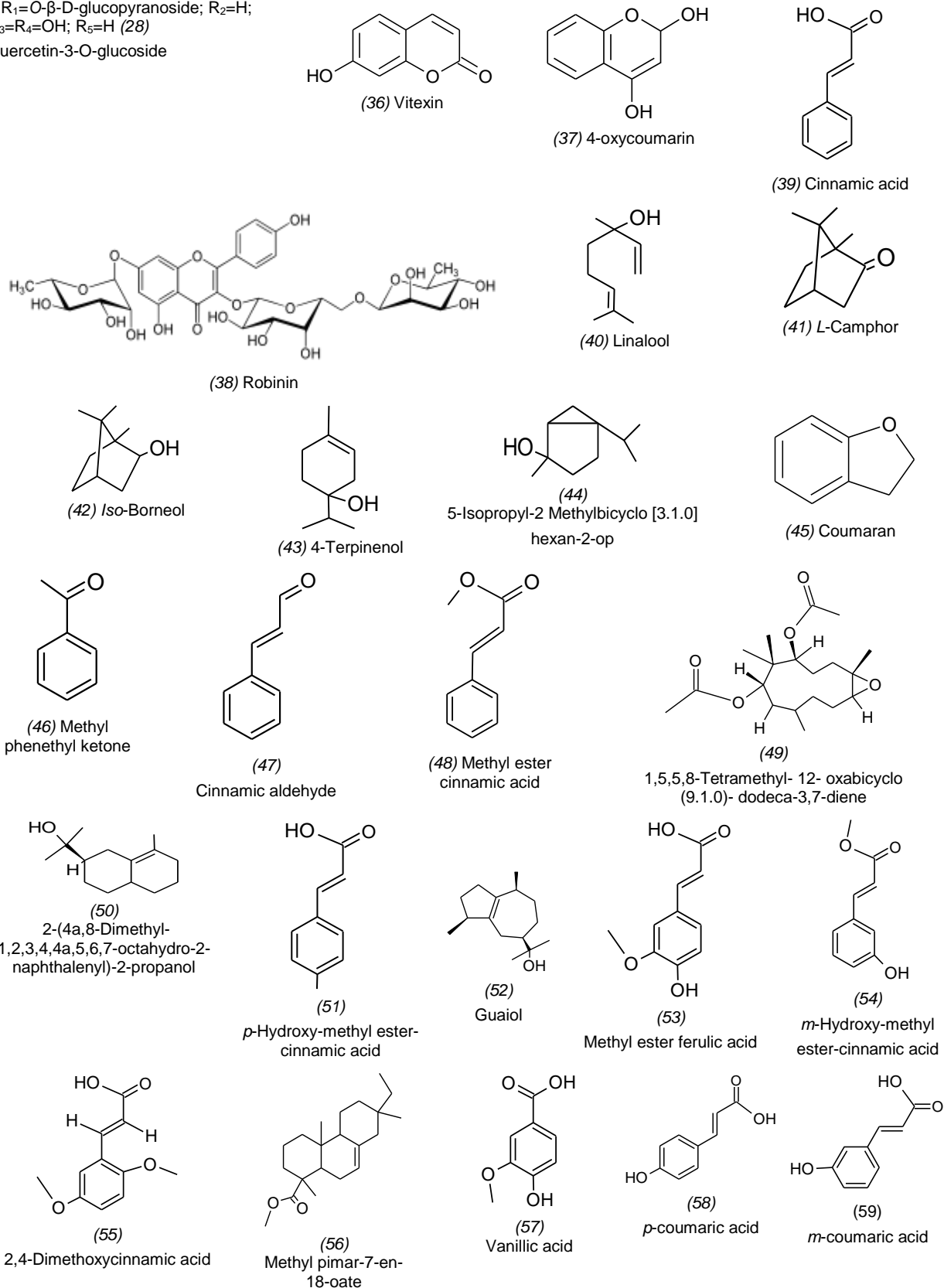


Figure 3. The structures of chemical constituents involved in allelochemical activities isolated and identified in barnyardgrass

Allelochemicals - Interactions between Barnyardgrass and Rice

In agroecosystem crops, surrounding plants, weeds, and microbes constitute the biotic components, which not only interact with each other but also with the abiotic environment through the use of phytotoxins produced by the biotic components or by the release of allelochemicals (Hoagland, 2001; Singh *et al.*, 2003). Therefore, the interactions of allelopathy and/or allelochemicals between barnyardgrass and rice need to be comprehended as important strategies for weed management. Rice (*O. sativa* L.) is a major food crop for more than half of the world's population, especially in South and Southeast Asia and Latin America. However, rice yields are significantly reduced each season with the highest loss potentially due to direct weed infestation. A total of 1800 species have been reported as weeds of rice in which *Echinochloa* spp. is dominant and has been recorded as a strong competitor with rice in many rice growing areas around the world (Rao *et al.*, 2007). Because barnyardgrass causes significant rice yield losses, much effort has been devoted to finding out the allelopathic/allelochemical interactions between rice and barnyardgrass, including the interference, competition, and allelopathic responses. However, very little information is currently available about the biological mechanisms of the allelochemical interaction between rice and barnyardgrass.

Allelochemicals - mediated allelopathic interaction between barnyardgrass and rice

In nature, plants release secondary metabolites in order to protect themselves under the certain abiotic and abiotic stresses. In last decades, many studies have reported that rice plants produce certain phytotoxic compounds (allelochemicals) to suppress the growth of barnyardgrass and nearby weeds in paddy fields. Contrarily, barnyardgrass has been shown to also release numerous allelochemicals to inhibit rice plants in paddy fields (Khanh *et al.*, 2008). For instance, momilactone A and B are labdane-related diterpenoids which are present in whole

rice parts (Kato *et al.*, 1973; Khanh *et al.*, 2007a), and are part of the gene cluster for the biosynthesis of the potent allelochemical 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one DIMBOA. A phytotoxin and momilactone A were also found in barnyardgrass (Guo *et al.*, 2007). Hence, there exists a controversy as to whether specific allelochemicals play a role in directly mediating antagonistic plant-plant allelopathic interactions (Xu *et al.*, 2011). Moreover, a role for specific secondary metabolites and allelopathic mechanisms in allelopathy have been ambiguous by the chemical complexity of root and plant litter exudates, as well as the interaction of these allelochemicals within the soil matrix and with associated microbes (Belz, 2007; Xu *et al.*, 2011). For example, the momilactones were originally isolated from rice and thought to act as plant growth inhibitors to suppress paddy weeds (Kato *et al.*, 1973; Kato-Noguchi, 2004; Chung *et al.*, 2006; Khanh *et al.*, 2007a). The amount of momilactones varied among rice germplasm, and depended on the environment and other conditions where rice was grown (Khanh *et al.*, 2007a). The allelopathic activity of barnyardgrass was reported to increase when grown with rice seedlings, whereas the concentration of a potent allelochemical, momilactone B, released from rice root exudates increased to suppress the growth of the barnyardgrass. This supports the observation that when rice and barnyardgrass plants were grown together, the allelopathic bioactivity of rice increased approximately 6.9-fold due to rice roots releasing the potent allelochemical, momilactone B (Kato-Noguchi, 2011). Similarly, Sun *et al.* (2012) qualified the growth-stimulating allantoin (5-uredohydantoin) which was released from rice root exudates but was not found in barnyardgrass. This may explain how barnyardgrass responds to the presence of nearby rice by sensing momilactone B in the exudates of rice roots and enhanced its allelopathic activity. Barnyardgrass allelopathy is most likely one of the inducible defence mechanisms initiated by chemical-mediated plant interactions between rice and barnyardgrass (Kato-Noguchi and Ino, 2013).

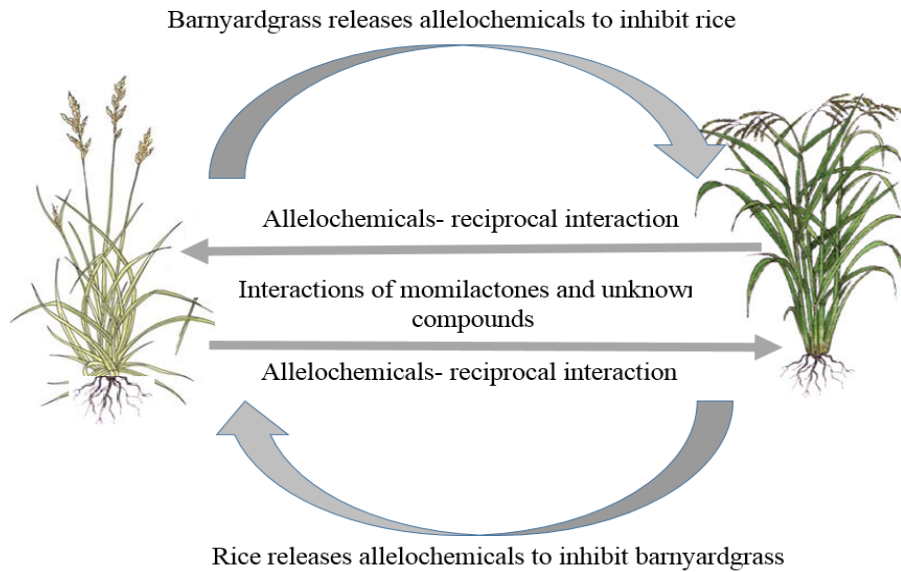


Figure 4. The proposed interaction of allelochemical pathway between barnyardgrass and rice

It is conferred during the evolutionary process that rice and barnyardgrass may have developed the ability to cross talk using chemicals to activate the defense mechanisms against some biotic stress conditions by detection of specific key compounds (Figure 4). However, the fate and actual modes of action for how the allelochemicals interact together between rice and barnyardgrass in nature remain obscure. Kato-Noguchi and Ino (2013) reported that when barnyardgrass and rice seedlings were grown together, the growth of both rice and barnyardgrass were reciprocally suppressed. While the allelopathic activity of barnyardgrass was enhanced by the presence of rice seedlings, the allelopathic activity of rice was also intensified as measured by the increase in allelochemical compounds from root exudates. The authors also proposed that rice seedlings may be aware of the presence of barnyardgrass allelochemicals which may trigger a signal cascade resulting in improved rice allelopathy via an increase in the amount of momilactone B. This suggests that both rice and barnyardgrass may have developed the chemical cross talk ability to promote defense mechanisms against abiotic stress conditions by reciprocal detection of certain key compounds (Kato-Noguchi and Ino, 2013). You and Wang (2010) examined the levels of exogenous jasmonic acid (JA) and salicylic acid (SA) in tissues and their

correlation to rice allelochemicals induced by the presence of barnyardgrass. The results showed that the allelochemicals of rice were promoted by coexisting with barnyardgrass and enhanced an allelopathic rice cultivar (IP312777), suggesting that JA and SA play an important role in the chemical communication between rice and barnyardgrass as well as participate in rice-barnyardgrass allelopathic interactions.

The potent allelochemical DIMBOA and phytotoxin momilactone A gene clusters have been found in the biosynthesis of barnyardgrass, of which DIMBOA was activated in response to co-cultivation with rice, while the momilactone A gene cluster was activated against blast disease (*Pyricularia oryzae*) (Guo *et al.*, 2017). Interestingly, DIMBOA showed significant enhancement in barnyardgrass co-cultivated with rice at three different time points (45 min, 1.5 h, and 3 h), which implied the rapid environmental adaptability of barnyardgrass for its survival and suppressing rice in the paddy fields.

Root exudates and allelochemical interactions between barnyardgrass and rice

Root exudation of living plant roots is a ubiquitous phenomenon in nature as a typical plant defense strategy, and mechanism of allelochemical release, occurring in the plant

kingdom through root hairs, which are individual cells involved in the synthesis and excretion of bioactive metabolites (Weston *et al.*, 2013; Zhu *et al.*, 2016). The soil-root interface (rhizosphere) is a complex environment with multiple activities occurring at the same time including a myriad of secondary metabolites being released by the living roots in the soil, plant material decomposing, and the actions of associated microorganisms (Latif *et al.*, 2017). The released allelochemicals are in mixtures and their concentrations are dependent on the plant itself, and affected by various abiotic and abiotic factors in nature. However, belowground interactions between root exudates and microbes are continuously occurring in the rhizosphere and are often difficult to study because of their presence in a complex soil matrix (Weston and Duke, 2003; Latif *et al.*, 2017).

In paddy fields, when rice and barnyardgrass grow together, rice responds to barnyardgrass stress by increasing the concentration of allelochemicals such as momilactone A, momilactone B, and phenolic acids, etc. to inhibit barnyardgrass (Kato-Noguchi, 2011; You *et al.*, 2011). Similarly, Kong *et al.* (2004b) reported that the synthesis of two compounds, 5,7,4'-trihydroxy-3',5'-dimethoxyflavone and a cyclohexenone (3-isopropyl-5-acetoxycyclohexene-2-one-1), were induced in rice by the presence of barnyardgrass. He *et al.* (2012) disclosed that the biosynthesis of phenolic compounds in rice was upregulated in the presence of barnyardgrass. However, it is unclear as to whether this phenomenon is due to biotic stress from the interference of barnyardgrass and/or the inducing effect of chemicals secreted by barnyardgrass. Barnyardgrass seed production was greater when seedlings emerged with rice (Zhang *et al.*, 2017b; Bagavathiannan *et al.* 2012), and root competition plays a major role in the interaction between barnyardgrass and rice (Assemat *et al.*, 1980). The recent study of Zhang *et al.* (2018) reported that the presence of allelopathic rice roots affected barnyardgrass root morphology, nutrient foraging, and competition, implying that allelopathy plays a

key role in root recognition behaviour of barnyardgrass-rice competitive interactions. Several hypotheses have been proposed to explain root recognition, including physical signalling, chemical signalling, and microorganism mediation (Falik *et al.*, 2003; Bais *et al.*, 2006; Zhang *et al.*, 2018). Many allelochemicals have been isolated and identified in all parts of both barnyardgrass and rice plants including leaves, stems, grains, husks, and root exudates (Table 1). Rice was known to mediate its allelochemicals to inhibit nearby weeds (Kong *et al.*, 2004a; Kato-Noguchi *et al.*, 2011). Contrarily, the root exudates of barnyardgrass release many growth inhibitor compounds which can cause inhibitory effects to rice and other plants. In nature, generally, after allelochemicals are released from the plants, they are involved in a variety of metabolic processes in plants (Singh *et al.*, 2003). The phytotoxic compounds are presented by their concentrations, flux rate, age and metabolic state of plant, and prevailing climatic and environmental conditions (Wyman-Simpson *et al.*, 1991; Nilsson *et al.*, 1998). However, the question is how those allelochemicals interact with one another in natural conditions and whether allelochemicals released from rice or barnyardgrass are sufficiently concentrated to inhibit each other. Even if a specific allelochemical was found in sufficient quantities in the rhizosphere of producer and receiver plants, it has been argued that allelochemicals have co-evolved in both plants (Weir *et al.*, 2004) as cost-effective strategies for symbiotic development over time in the environment. The different classes of allelochemicals are involved in these interactions, and lead to multiple modes of allelochemical actions against target species.

However, Olofdotter *et al.* (2002) reported that the concentration of allelochemicals released by rice root exudates cannot reach the phytotoxic level for weed inhibition in paddy fields because plant allelochemicals are often present at very low concentrations, are transient, and are affected by multifaced climatic, environmental conditions and edaphic factors. As a matter of fact, many allelopathic rice cultivars have been identified using artificially prepared extracts or exudates concentrations,

which cannot be produced under field conditions (Belz *et al.*, 2005; Khanh *et al.*, 2007a; Abbas *et al.*, 2017). A diverse repertoire of allelochemicals are released by both rice and barnyardgrass, and are affected by surrounding environmental factors in paddy fields including pH, water, light, temperature, space, and macro- and micronutrients, causing lower concentrations which are ascertained as hormesis to boost plant growth over time. This helps explain why it is difficult to develop allelopathic rice in practice. In the view of biological and physiological mechanisms mediated by allelochemicals, several previous studies proposed that the phytotoxic mechanisms induced by allelochemicals are the inhibitions of photosynthesis and oxygen evolution via interactions with components of photosystem II (PSII) (Einhellig *et al.*, 1993; Rimando *et al.*, 1998), of which some allelochemicals are responsible for disrupting normal metabolic processes in the plant. Some allelochemicals may interact with the mitochondrial membrane and impair mitochondrial respiration directly. One of the interactions between plants and allelochemicals is allocated in a more dynamic ecological situation, some factors may interact to influence the phytotoxicity of allelochemicals (Weir *et al.*, 2004). In the case of root exudates of barnyardgrass, they may possess the signal molecules which can induce increases in rice allelochemicals (Metlen *et al.*, 2009; Kato-Noguchi and Ino, 2013). However, it is difficult to conclude if the transfer of allelochemicals is soil-mediated or how much is directly transferred through actual root-root contact (Inderjit *et al.*, 2005). Moreover, root growth of both rice and barnyardgrass may be indirectly affected by root-soil microbial interactions mediated by root exudates, and by the joint actions of multiple allelochemicals rather than one specific chemical because the exudation of roots can either enhance or diminish soil nutrient availability by altering the rhizosphere microbial community and the chemical properties (Bertin *et al.*, 2003; Khanh *et al.*, 2007b; Kato-Noguchi and Ino, 2013; Wang *et al.*, 2013; Zhang *et al.*, 2018). Allelopathic

activities may also be due to the joint actions of allelochemicals and their interactions with other organic compounds present in the soil substratum (Blum, 1996; Inderjit *et al.*, 2002). Both rice and barnyardgrass are semi-aquatic and are typically grown under partially flooded conditions. Therefore, it is difficult to elucidate allelochemical interactions in field conditions. Also, paddy soil properties and edaphic effects may play key roles affecting the extent of allelopathic interactions over time in the rhizosphere of both barnyardgrass and rice.

Conclusions and Future Lines of Research

Most of the studies on the allelochemicals of barnyardgrass have shown that this weed has allelopathic potential and releases numerous inhibitor substances into the environment during its growth and development. These substances inhibit the growth of rice and vicinity plants, depending on the density of the grass in paddy fields. Prospective research should focus on the following: (1) further evaluation of the specific interactions *in vitro* and *in vivo* to identify the specific allelochemical pathways; (2) allelochemical interactions between rice and barnyardgrass in paddy field should be judiciously studied to further (3) demonstrate the mechanisms of allelochemicals in root-root interactions and chemical communication below ground as well as (4) study the signal molecules in exudations of rice and barnyardgrass and their functions; (5) call for multidisciplinary global research on plant ecology, genetics, physiology, biochemistry, soil science, and microbiology to further the work on allelochemical interactions of rice and barnyardgrass in the soil rhizosphere.

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