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Review

Rice allelopathy in weed management – An integrated approach

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Abstract: The intensive use of pesticides with low biodegradability and high persistence in soil, surface and ground waters, represents a considerable environmental risk, especially under high weed pressure conditions. Furthermore, the number of herbicide-resistant weeds is increasing. Against this background, the investigation of alternative weed control strategies has taken on considerable importance. Among these, allelopathy as a negative effect of one plant on another due to the direct or indirect (including microorganisms) release of chemicals in the environment can be a useful tool for the integrated management of weeds in agroecosystems. In particular, the paddies have been considered in this work by reviewing the data both on rice allelopathy and rice weed agronomic control methods developed to improve the crop yield.

Key words: Herbicides; Allelochemicals; Phytotoxicity; Paddy.

Introduction

The agricultural use of pesticides as crop protection products against plant diseases, harmful insects or weeds is one of the main causes of water pollution and soil contamination. Over 95% of the herbicides reach a destination other than their target species, including non-target-species, air, water and soil with possible serious human health consequences (1-3).

At the same time, globally, 254 plant species have evolved resistance to 23 of the 26 known herbicide sites of action and to 163 different herbicides. Herbicide resistant weeds have been reported in 92 crops in 70 countries. In particular, herbicide resistance weeds in rice are 51 in 30 countries (http://www.weedscience.org/Summary/Herbicide.aspx).

On these grounds, several alternatives to pesticides have been proposed, some of which proved to be equally effective and without ecological impacts in countries of application (4). Among the integrated weed control practices, allelopathy could be a useful tool to develop new eco-friendly management approaches. It is a concept known since ancient times. Democritus (460-370, BC), Theophrastus (371-287, BC) and Pliny (23-79, AC) reported examples of plants producing phytotoxic substances able to prevent the growth of other plants in the same soil (5, 6). On the other hand, the allelopathy term was introduced in 1937 by Hans Molisch to describe the influence of one plant on another through the delivery of chemicals into the environment (7). Afterwards, in 1984, Elroy Leon Rice enlarged the definition to include all direct positive or negative effects of a plant on another plant or on microorganisms by the liberation of biochemicals into the natural environment (8). Currently, according to the International Allelopathy Society, allelopathy refers to the impact of plants upon neighbouring plants and/or their associated microflora and/or macrofauna by the production of allelochemicals which may have harmful effects (inhibition) or benefits (stimulation) on plant growth (http://allelopathy-society.osupytheas.fr/). Anyway, it is an interference mechanism playing an important role in natural and managed ecosystems through strategies based on the use both of phytotoxins released by living or dead plants and of crop phytotoxic residues or mulches (9, 10). For allelopathy to be an ecologically relevant mechanism in influencing the plant growth in field conditions, chemicals have to accumulate and persist in the soil at phytotoxic levels and reach the target plants (11). Allelopathic effects are largely determined by the amount of exuded chemicals; by the chemical, physical, and microbial components of soil; by the replenishment of allelochemicals and the responses of neighbouring species (12).

Reports on the allelopathy of crop species can be traced back to ancient times, while works on genetic variability of allelopathy in crop cultivars as an option for breeding weed suppressive cultivars with improved allelopathic traits have a short history (10). Starting with the evaluation of *Cucumis sativus* L. for varietal allelopathic activity (13), several other crops followed, e.g. *Avena sativa* L. (14), *Triticum aestivum* L. (15), *Hordeum vulgare* L. (16), *Secale cereale* L. (17, 18), *Sorghum* spp. (19, 20), and *Oryza sativa* L. (21).

Studies on rice allelopathy, started in the early 70s, have been widely conducted in the USA, Europe, Japan, Korea, India and China (22). Cultivars with elevated allelopathic activity can be beneficial in reducing need for commercial herbicides at least at early season application, because at late season weed control is provided by the competitiveness of crop itself (23).

Reducing weed infestation by exploiting the allelopathic properties of rice may be the most important goal and has been a hope of many agronomists. The direct use of rice residues and genetic control of rice allelopathy via breeding programmes to enhance weed suppression may be the most feasible strategy (22).

In this review, we document some weed management approaches like the use of rice allelopathy and of other agronomic control methods employed to improve the yield of rice itself.

Rice allelopathy

Rice allelopathy is a quantitative trait, which is mediated by both genetic background and environmental conditions (24, 25). Studies have shown that it is an inducible trait influenced both by biotic and abiotic stress factors like nutrient starvation and higher accompanying weed densities (24, 26, 27). Suitable allelopathic traits include early seedling emergence and seedling vigour. In addition, fast growth rates producing a dense canopy, greater plant height, higher root volume and longer growth duration are characteristics known to increase the ability of rice cultivars to compete with weeds (28). Plant height is often described as one of the most important factors in the competitive ability of a crop (29, 30).

For adaptation to both moderate and severe weed pressure, genotypes should have high-yielding ability and, at early growth stages, rapid increase in plant height, high number of tillers and higher leaf area index (LAI). Besides these, high nitrogen and chlorophyll content can be considered as an important trait for selection of competitive genotype (31).

The use of rice residues in paddy fields themselves has long been recognised as an important source to improve the organic matter status of soil and was also reported to reduce the emergence of weeds. As an example, it was shown that residues of rice (cv. Sarjoo 52) mixed with the soil (5-6 cm in depth, 5 tons ha^{-1}) suppressed *Echinochloa colona* (L.) Link, *Ammania baccifera* L., *Ammania multiflora* Roxb., and *Phyllanthus fraternus* G.L.Webster (32). The only rice straw inhibited *Phalaris minor* Retz. growth by influencing soil chemical and/or microbiological properties (33). Leaf plus straw and hulls of some rice cultivars with strong allelopathic property prevented weed interference by 60–95% (34). Xuan *et al*. (35) noted that rice hulls and bran, each at 1 ton ha^{-1}, reduced paddy weed biomass by about 25% and 50%, respectively. The combined application of rice by-products and *Medicago sativa* L. strengthened weed suppression by 70-80% and was more effective than either used singly. Other experiments reported that rice straw and stubbles stopped the germination of *A. sativa*, *T. aestivum*, *Convolvulus arvensis* L., *Avena ludoviciana* Durieu, *P. minor* and *Lens* spp. (36). The decomposition of the same rice residues has reduced the occurrence of both broad-leaved and grassy weeds (37). The application of rice straw waste simultaneously or 3 months before sowing of *C. sativus* gave promising results in suppressing growth and development of a wide range of broad- and narrow-leaved weeds increasing, at the same time, the crop yield productivity (38).

Furthermore, weed-suppressive effects of rice varieties have been studied. They improved with increase in planting density, flooding depth (3-12 cm), flooding duration (5-15 days) and supply of nitrogen (105-210 and 315 kg ha^{-1}) (39). Rice plant characteristics that impart weed competitiveness include plant height, quick canopy development, profuse tillering, horizontal-leaf configuration with higher LAI and specific leaf area, and greater dry matter production prior to reproductive phase (40, 41). Again, the option to use a single allelopathic variety enhances weed suppression of around 10-20% while integrated management options including allelopathic rice varieties plus a low-dose herbicide application (bensulfuron-methyl, 25 g AI ha^{-1}, a third of the recommended dose) completely controlled the emergence and growth of most paddy weeds (41).

Rice allelochemicals

The term “allelochemical” relates to the role that a compound plays, but not to the actual chemical identity (42). Allelochemicals become stressful only when are toxic or affect the growth and development of surrounding plants (phytotoxicity) (43). To have some effect on the target plant, they have to be released from the donor plant. This can happen in different ways such as *i*) leaching from leaves and stem, *ii*) volatilization from the green parts, *iii*) release from degrading material or *iv*) from roots as exudates (44) (Figure 1).

In plants, the allelochemicals can be present in leaves, flowers, fruits, bark and roots. To reach the rhizosphere, these molecules have to be mobile or rather soluble in water (45). Their action in target plant is diverse and affects a large number of biochemical reactions resulting in modifications of a variety of morpho-physiological processes (46). Indeed, the effects of allelochemicals are detected at biochemical, molecular, physiological and structural level of the plant organization (47) (Table 1).

Accordingly, the activity of allelochemicals cannot been explained by just a single mode of action. The majority of effects, such as reduction in seed germinability and seedling growth, chlorosis, decreased ion uptake, other physiological, morphological and anatomical abnormalities are caused by a variety of specific interactions between allelochemicals and cellular or molecular targets still not completely understood. Allelochemicals

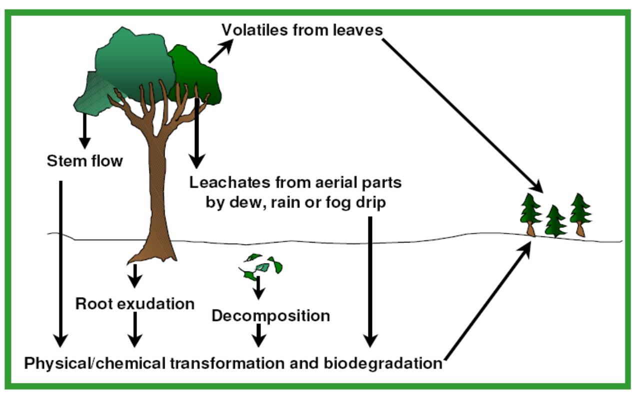


Figure 1. Possible ways of allelochemical release

Table 1. Multilevel action of allelochemicals (47).

Action level in plant	Effects
Biochemical and molecular	Decreased synthesis of DNA, RNA and housekeeping proteins Increased synthesis of stress proteins and metabolites
Physiological	Alterations in photosynthesis Mitochondrial respiration Ion uptake Growth Development
Structural	Alteration of cell ultrastructure Mitosis inhibition

are also involved in altering the micro- and ultrastructure of plant cell as well as of the nucleic acid and protein biosyntheses, cell redox homeostasis and levels of plant growth regulators.

Not least, the effects of allochemicals on microbial community have to be taken into account (48).

The chemical structure of organic compounds that mediate these interactions is as diverse as their modes of action. Most plant chemicals involved in allelopathic activity are secondary metabolites from the shikimic acid or acetate pathways able to influence many primary metabolic processes and growth regulatory systems in higher plants (49, 50). Compounds of several chemical classes such as fatty acids, benzoxazinoids, indoles, phenolic acids, phenylalkanoic acids and terpenoids are considered allelochemicals (51).

Modern analytical instruments like GC-MS, LC-MS, NMR and IR have helped to either identify or confirm various allelochemicals as cytokinins, phenols, indoles, terpenic acid, phenylalkanoic acids, sterols, benzaldehydes, benzene derivatives and long-chain fatty acids and their esters and ketones (49, 52-55).

Among detected phenolic acids, *p*-hydroxybenzoic, vanillic, *p*-coumaric and ferulic acids are the most common rice allelochemicals (49, 52, 53, 56-58). Table 2 shows some of the basic plant secondary metabolites identified as rice allelochemicals (59, 60).

Allelochemicals released by rice inhibit the weed species but they are not inhibitory to the rice itself. Olofsdotter *et al.* (61) compared rice cultivars with two *Echinochloa* species, and a significant difference in their tolerance of *p*-hydroxybenzoic acid was reported. The weeds exhibited half ED_{50} values compared to those of the rice samples. These results showed that the considered allelochemical selectively controls the *Echinochloa* species at a concentration not affecting the rice growth and suggested a possible evolutionary pressure in rice towards the tolerance of phenolic acids and the prevention of autotoxicity.

A conserved mechanism to prevent autotoxicity involves the induction of detoxifying enzymes and transporters of recognition of xenobiotic compounds, thereby facilitating their inactivation and elimination. Classically, this process is divided into three phases as follows.

In phase I, compounds are typically modified such that a functional group such as the hydroxyl moiety is added or exposed through the action of hydrolases, cytochrome P450s, or peroxidases. In phase II, the availability of functional groups facilitates the formation of glucosyl, glutathione and malonyl conjugates through the action of specific glucosyltransferases, glutathione S-transferases and, less frequently, malonyltransferases.

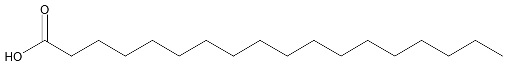
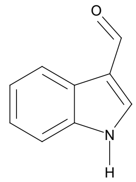
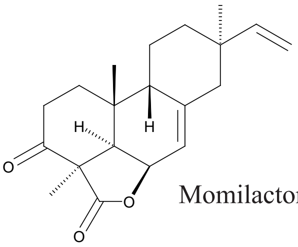
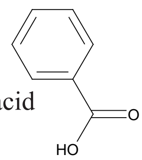
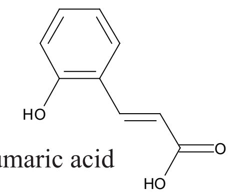
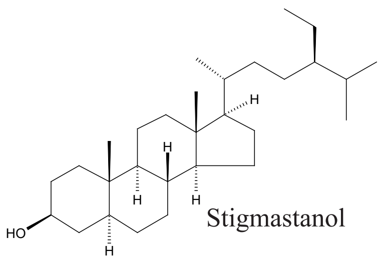
In phase III, conjugated forms of xenobiotics can then be recognized by specific membrane-associated transporters such as ABC transporters, resulting in their vacuolar sequestration or release into the apoplastic space via exocytosis.

Molecular approach

Allelopathy is one of the last areas of plant science to use molecular biology as a tool in understanding the phenomena. Allelopathic competition, defined as the unequal sharing of resources such as nutrients, light and water, is dependent on several physiological and phenological traits (62, 63). For breeding crops with high allelopathic potential, it is crucial to know which genes are involved in crop competitiveness and phytotoxicity. Molecular marker-aided genetics is presently an optimal tool for identifying quantitative traits, mapping the genes involved with a reasonable level of precision and analysing the relationship between traits of interest and other important agronomic traits (62). The selection of rice cultivars with high weed suppression ability through transgenic and breeding programmes can useful in weed biological control field.

The allelopathic activity of rice varies among cultivars. It was proposed that it is related to some growth characteristics, but also that may be a polygenic trait feebly correlated with yield or other agronomic features. Allelopathic potential in rice was demonstrated to be quantitatively inherited, but the allelopathic traits were not identified (63). Despite research on rice allelopathy dates back to the early 1970s, a genetic approach started only in 1996 (64). Dilday *et al*. (65) crossed the allelopathic rice cultivar PI312777 with another non-allelopathic rice cultivar Lemont and noted that the F2 was effective against *Heteranthera limosa* (Sw.) Willd. and was quantitatively inherited. Jensen *et al*. (66) studied quantitative trait loci (QTLs) mapping using a population of 142 recombinant inbred lines (RILs) derived from a cross between IAC 165 (Japonica upland cultivar) and CO 39 (Indica irrigated cultivar). Four main QTLs located on three chromosomes, 2, 3 and 8, were identified and claimed 35% of the total phenotypic variation of the allelopathic activity against *Echinochloa crus-galli* (L.) P.Beauv. Okuno & Ebana (67) identified seven QTLs controlling rice allelopathy on chromosomes 1, 3, 5, 6, 7, 11 and 12. Ebana *et al*. (68) also identified QTL genes associated with the effect by using restriction fragment length polymorphism markers. One of the QTLs on chromosome 6 had the largest effect, explaining 16.1% of the phenotypic variation. He *et al*. (23) employed proteomic methods to study the molecular mechanism of crop allelopathy and identified four

Table 2. Main allelochemicals identified from rice (22).

Chemical class	Constituents	Representative structure	Occurrence
Cytokinins	Cytokinins		Root exudates
Fatty acids	Stearic acid Azelaic acid	 Stearic acid	Soil
Indoles	1H-indole-3-carboxaldehyde 1H-indole-3-carboxylic acid 1H-indole-5-carboxylic acid Indole-5-carboxylic acid	 1H-Indole-3-carboxaldehyde	Root exudates
Momilactones	Momilactone A and B	 Momilactone A	Hulls, leaves and straw; root exudates
Phenolic acids	Benzoic acid Caffeic acid Ferulic acid *m*-Coumaric acid *o*-Coumaric acid *p*-Coumaric acid *t*-Coumaric acid Gallic acid Gentisic acid *p*-Hydroxybenzoic acid Salicylic acid Protocatechuic acid Mandellic acid Synapic acid Vanillic acid Syringic acid	Benzoic acid  *o*-Coumaric acid 	Straw, decomposed straw, root exudates, leaves and stem, soil, hulls
Steroids	Stigmastanol Ergosterol peroxide 7-Oxo-stigmasterol	 Stigmastanol	Hulls, fresh roots and aerial parts
Other constituents	1,2-Benzenedicarboxylic acid bis (2-ethylhexyl)ester 2-Methyl-1,4-benzenedio 1-Phenyl-2-hydroxy-3,7-dimethyl-11-aldehydic-tetradecane-2-b-D-glucopyranoside 3-Hydroxy-4-methoxybenzoic acid 3-Isopropyl-5-acetoxycyclohexene-2-one-1 4-Ethylbenzaldehyde 2- and 4-Hydroxyphenylacetic acid 5-Hydroxyindole-3-acetic acid 4-Phenylbutyric acid Abietic acid Lanast-7,9(11)-dien3a,15a-diol-3a-D-glucofuranoside Resorcinols		Root exudates, hulls, hull extracts, soil, straw

proteins involved in the production of allelochemicals: peroxidase precursor, thioredoxin M-type, 3-hydroxy-3-methylglutaryl-coenzyme-A reductase 3, and phenylalanine ammonia-lyase (PAL). The genes encoding these four allelopathy-related proteins are located on chromosomes 4, 7, 8, and 12.

In order to regulate gene expression, the first requirement is to identify the target allelochemical(s), to determine enzymes and the genes encoding them in order to insert a specific promoter in crop plants to enhance allelochemical production.

The highest content of *p*-coumaric acid (among other intermediates of the phenylpropanoid pathway) was found in several allelopathic rice cultivars. Cinnamic acid 4-hydroxylase (CA4H) is the enzyme catalyzing the conversion of cinnamic acid to *p*-coumaric acid, a key reaction in the biosynthesis of a large number of phenolic compounds in higher plants. Thus, modulating the activity of CA4H could enhance the production of allelochemicals (69). Studies have also been conducted to investigate specific promoters that can confer responsiveness on environmental stresses and plant-plant interaction. If a promoter is specifically responsive to an elicitor, it can be used to regulate genes involved in allelopathy.

Saito *et al*. (70) identified plant characteristics like grain yield, plant height at maturity and visual growth vigour at 42-63 days after sowing (DAS) that can be used as selection criteria for developing superior weed competitive rice genotype. Plant height, tiller number and LAI at 43 DAS were also identified as potential traits for selection of weed competitive rice genotypes (71).

Allelopathy limitations

Although allelopathy obtained promising results as a weed control tool in many situations, it has some limitations.

Plant age, nutritional status, temperature, light and herbicide treatments affect the production and release of allelochemicals. In addition, some abiotic and biotic soil factors may change the phytotoxic levels of allelochemicals. The activity of these compounds can be modified by physical, chemical and biological properties of soil, where processes such as retention (sorption), transport and microbial degradation/transformation (72) determine their persistence and fate. The microorganisms metabolize allelochemicals and their metabolites can be more or less phytotoxic than starting compounds (72). For example, the degraded products are often more phytotoxic. The fate of benzoxazinones from microbial degradation was investigated (10, 73). *T. aestivum* and *S. cereale* synthesize and exude at least two bioactive benzoxazinoids (DIBOA and DIMBOA). Both compounds are directly active on target species but are also rapidly degraded once released into soil due to both chemical and biological conditions, especially initial concentration, soil type and rhizosphere microorganisms. The corresponding obtained metabolites spontaneously produced in aqueous solution or by biological processes are the corresponding benzoxazolinones (BOA and MBOA), less phytotoxic than their precursors but still effective. Their microbial transformation leads to the formation of two persistent and bioactive aminophenoxazinones (APO and AMPO), further acetylated to form a fourth group of other active metabolites (AAPO and AAMPO). APO proved to be the most phytotoxic and persistent compound in the DIBOA degradation pathway, while the degradation of DIMBOA immediately results in a gradual loss of phytotoxicity. The formation of further metabolites with low or no phytotoxicity occurs in both degradation pathways (73).

Actinetobacter calcoaceticus, a gram-negative bacterium, was isolated from *S. cereale* crop soil and reported to convert 2(3H)-benzoxazolinone (BOA) to 2,2-oxo-l,l-azobenzene (AZOB) (74). Compared to BOA, AZOB was more effective in inhibiting *Lepidium sativum* L. and *E. crus-galli* (73). Gagliardo *et al.* (75) observed 50% inhibition in the radicle growth of *E. crus-galli* by 0.7 and 0.1 mM of BOA and aminophenoxazinone, respectively, showing the higher phytotoxicity of degraded product than its precursor BOA.

The autotoxic effect is another limitation in the mechanism of allelopathy. For instance, different identified autotoxins, including some derivatives of benzoic and cinnamic acids from the *C. sativus* root exudates, were investigated. The exudates and aqueous extracts exhibited inhibitory effects on root antioxidant enzymes and leaf photosynthesis, transpiration and stomatal conductance in *C. sativus* itself (76).

Therefore, when studying the allelopathic potential of a plant, the role of soil should not be ignored, though many studies on allelopathy were carried out on artificial substrate rather than soil.

Agronomic practices for rice weed management

O. sativa serves as basis of life for half of the world's population. About 90% of the world's rice grows and is consumed in Asia, with consumption as high as 990 g per person per day in some areas (77). Considering its importance as human food, it is one of the most important crop plant on earth (78). Rice is cultivated under many different environments, conditions and production systems, including 57% on irrigated land, 25% on rainfed low lands, 10% on uplands, 6% in deep water, and 2% in tidal wet lands (79). Rice production worldwide suffers from severe weed infestations causing serious yield losses, from 30 to about 100%, besides increasing production costs and deteriorating quality (67).

Dominating weed species include both annual and perennial grasses, broad-leaved plants and sedges. In upland rice ecosystem, hand weeding is the most common practice to control them. However, it requires more than 100-person per day ha^{-1}, is extremely laborious and time-consuming thus resulting very expensive (80). Therefore, despite its effectiveness, the manual weeding has been replaced by chemical control methods. Currently, in the rice production, herbicides account for the highest agricultural chemical input. According to Stephenson (81), most agricultural systems collectively use three million tons of herbicides per year. Their accumulation in soil and water is a threat to environment and may also lead to adverse effects on human health after entering the food chain.

Moreover, the development of herbicide resistance in weeds can endanger the ecosystem. The main herbicide resistant weeds worldwide include propanil-resistant *E. colona* in central and South America and *E. crus-galli* populations in the USA. In Malaysian agriculture, 18 herbicide-resistant weed species have been recognized since 1980. For example, *Eleusine indica* (L.) Gaertn. has developed resistance to the inhibitors of acetyl CoA carboxylase, while *Monochoria vaginalis* (Burm.f.) C.Presl to ALS inhibitors (82). Other weed species may also develop resistance in the future making the improvement of weed control more difficult.

Table 3. Prevalent weeds in paddy fields and detected herbicide resistance.

Family Species	Herbicide resistance		
	Detection's first year	**Country**	**Site of action**
Monocots Cyperaceae			
Cyperus difformis L.	1993	USA (California)	ALS inhibitors (B/2)
Cyperus iria L.	2010	USA (Arkansas)	ALS inhibitors (B/2)
Cyperus rotundus L.			
Fimbrystilis littoralis Gaudich.			
Scirpus juncoides Roxb.			
Scirpus planiculmis F.Schmidt			
Poaceae			
Cynodon dactylon (L.) Pers.			
Echinochloa colona (L.) Link	1987	Costa Rica	PSII inhibitor (ureas and amides) (C2/7)
Echinochloa crus-galli var. *crus-galli* (L.) P.Beauv.	1986	Greece	PSII inhibitor (ureas and amides) (C2/7)
Echinochloa glabrescens Munro ex Hook.f.			
*Eleusine indica (*L.) Gaertn.			
Ischaemum rugosum Salisb.	2000	Colombia	ACCase inhibitors (A/1)
Leptochloa chinensis (Roth) Nees	2002	Thailand	ACCase inhibitors (A/1)
Oryza sativa var. *sylvatica*	2002	USA (Arkansas)	ALS inhibitors (B/2)
Paspalum distichum L.			
Rottboellia cochinchinensis (Lour.) Clayton			
Dicots			
Alismataceae			
Sagittaria pygmaea Miq.	2004	South Korea	ALS inhibitors (B/2)
Asteraceae			
Eclipta prostrata L.			
Onagraceae			
Ludwigia prostrata Roxb.	2011	South Korea	ALS inhibitors (B/2)
Pontederiaceae			
Monochoria vaginalis C.Presl	1998	Japan	ALS inhibitors (B/2)
Potamogetonaceae			
Potamogeton distinctus A. Benn.			

Data retrieved on May 4, 2018 from International Survey of Herbicides Resistant Weeds available at http://www.weedscience.org. ALS inhibitors (B/2): Group B/2 herbicides inhibiting acetolactate synthase; ACCase inhibitors (A/1): Group A/1 herbicides inhibiting acetyl CoA carboxylase; PSII inhibitor (ureas and amides) (C2/7): Group C2/7 herbicides inhibiting photosynthesis at photosystem II.

Rice weeds

In field conditions, weeds compete with rice for light, nutrients, water and other growth requirements. They pose an important biological constraint to rice productivity (83). The dimension of weed infestation varies, depending on the predominant weed flora and on the control methods practiced by farmers. In China, 10 million tons of rice are lost annually due to weed competition, a quantity sufficient to feed at least 56 million people for 1 year (84). In Sri Lanka, a country considered self-sufficient in rice, the weeds are the main biotic stress in its production by causing yield losses from 30 to 40 %. The dominant weed species in paddy fields worldwide are shown in Table 3. Weeds infesting lowland rice system include annual grasses (*E. crus-galli, E. colona*), annual broad-leaved plants (*M. vaginalis, Ludwigia parviflora* Roxb.*, Marsilea quadriflora* L.), annual sedges (*Cyperus difformis* L., *Cyperus iria* L., *Fimbristylis milacea* (L.) Vahl), perennial grasses (*Panicum repens* L., *Paspalum conjugatum* P.J.Bergius) and perennial sedges (*Scirpus martimus* L.). Weeds infesting upland rice system include annual grasses (*E. colona, Digitaria sanguinalis* (L.) Scop.*, E. indica, Dactyloctenium aegyptium* (L.) Willd.), annual broad-leaved plants (*Amaranthus spinosus* L., *Ageratum conyzoides* (L.) L., *Celosia argentea* L.*, Commelina benghalensis* L., *Eclipta alba* (L.) Hassk.*, Portulaca oleracea* L.*, Trianthema portulacastrum* L.), annual sedges (C. *iria*), perennial grasses (*Imperata cylindrica* (L.) Raeusch., *Cynodon dactylon* (L.) Pers.) and perennial sedges (*Cyperus rotundus* L.).

Damasonium minus (R.Br.) Buchenau is, economically, one of the most important rice weeds in Australia. It belongs to the family Alismataceae, which also encompasses several other important rice weeds such as *C. difformis*, *Sagittaria montevidensis* Cham. & Schltdl., *Stellaria graminea* L., *Alisma plantago-aquatica* L. and *Alisma lanceolatum* With. (85). Besides these, several other weed species have also been reported in paddy, namely *Heteranthera limosa* (Sw.) Willd., *Ammannia coccinea* Rottb., *Brachiaria platyphylla* (Munro ex C.Wright) Nash, *C. iria*, *E. crus-galli, Chenopodium* *album* L. and *Leptochloa* spp. (67).

E. colona and *E. crus-galli* C4 plants are among the world's most serious rice grass weeds. Both species resemble rice at the seedling stage, but, by the time, weeds can be easily recognized and removed by farmers, even if the crop yield loss may already be unavoidable (86). Rabbani *et al*. (87) reported *E. colona* to be the most damaging weed in rice, causing a yield loss of 56% in Basmati-385 and 42% in Super Basmati.

To solve problems related to weed abundance in rice, it is necessary to develop sustainable weed management systems that may reduce both herbicide dependency and the burden of manual weeding.

It has been demonstrated that application of several plants (e.g., Fabaceae and Passifloraceae) with strong allelopathic ability to paddy soils at 1–2 tons ha^{-1}, immediately after transplanting, can reduce the initial growth of weeds by up to 80% (35, 88-90). In addition to this, cultural management practices also influence the weed control in rice cultivation. A method followed to reduce the effects of weeds on the crop, is either by making weeds less competitive or by making the crop more competitive (91). Johnson *et al*. (92) reported 40-48% reduction in rice grain yield when weeds emerged with the crop, as compared to when weeds were controlled until 42 day after sowing. These results concur with those of other authors (93-95) which also suggested that narrowing of row spacing can reduces the weed seed production. Late-emerging weed seedlings are generally less competitive and produce less biomass and fewer seeds than early-emerging seedlings (96). The delay in weed emergence by only 15 days compared to the crop led to at least 15% greater rice grain yield. It was further improved (30-40%) when weed emergence was delayed until 45 days after that of rice.

Late-emerging weed seedlings would be expected to suffer more from shading than early-emerging weeds, and this differential effect may help explain differences in seed production (95). These reductions in growth and seed number due to competition for light have also been reported for other weed species (97, 98). A change in light quality due to the presence of canopy cover can affect the development of shaded plants through phytochrome-mediated processes. Some authors suggested that, for weed growth reduction, shading by the crop would have to occur early in the season (98, 99).

The seedling density is another important factor in rice management practices. The yield losses are expected to be very high with seeding rates of 15-20 kg ha^{-1} generally prescribed for growing dry seeded rice in India, if weed control measures are not adopted. With a seed rate of 50 kg ha-1, the weed competition reduced the yield by about 50% (100, 101). It has been demonstrated that, at the same seeding rate, the weed count and biomass of *E. crus-galli* and *Cyperus rotundus* L. were minimum while at lower seeding rate of 20-30 kg ha-1 were maximum (102). In Philippines, increasing seed rate from 25 to 100 kg ha^{-1} diminished the average weed biomass at crop harvest by 53%, while, in India, the reduction was 49% at 4 weeks after planting (103).

Future scope of research

Although several aspects of allelopathy have already been investigated and some studies are still in progress, some other areas need to be explored extensively to clarify its complex mechanisms.

For optimal use of allelopathy under field conditions, the influence of environmental factors needs to be considered. In this concern, soil environment is the most important factor. The interaction of allelochemicals with different soil properties is pivotal. From agronomic point of view, allelopathy deserves much attention. Several agronomic practices, such as method of sowing or transplanting (for rice wet-seeded or dry-seeded), spacing of crop, seed rate, timing and source (organic, inorganic or integrated) of nutrient application, method, time and frequency of irrigation create different situations for establishment and growth both of crop plants and weeds, thereby influencing allelopathy efficacy.

In case of use of allelochemicals as natural herbicides, their correct identification and possible residual effects, on both crops and weeds, have to be explored to avoid agronomic problems and to select suitable crop management practices such as crop rotation and cropping system. In addition, their movement, transportation, half-life, biodegradability, interaction with other chemicals in soil should be taken under consideration as well as their uptake by target plant and mode of action. Finally, identification of genes encoding for allelopathy in different plants is required.

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