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Upland Rice and Allelopathy

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ABSTRACT

Upland rice (*Oryza sativa* L.) is mainly grown in Asia, Africa and Latin America. Yield potential of upland rice is quite low and invariably this crop is subjected to many environmental stresses. Further, when upland rice is grown in monoculture for more than two to three years on the same land, allelopathy or autotoxicity is frequently reported. Allelopathy involves complex plant and plant chemical interactions. The level of phytotoxicity of allelochemicals is influenced by abiotic and biotic soil factors. Adopting suitable management strategies in crop rotation can reduce or eliminate allelochemicals phytotoxicity. Rice yields can be improved by growing rice in rotation with other crop species. Allelochemicals of rice can be used for control of weeds in this crop as well as other crops that are grown in rotation with rice. This review highlights that present knowledge of allelopathy in upland rice is inadequate and fragmentary, and therefore, more controlled

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and field studies are needed to understand and to reduce the detrimental effects of allelopathy in the upland rice production.

Key Words: Allelochemicals; Weed control; Crop rotation; Resistant cultivars; Nutrient supply; Rice.

INTRODUCTION

Rice is a staple food for more than 50% of the world's population. It is grown in both dryland and wetland conditions, over a wide range of latitudes. Upland rice refers to rice grown on rainfed and naturally well-drained soils having undulated topography.[1] Upland rice is grown annually on about 17 million ha of land area worldwide, and this represents about 10.5 million ha in Asia, 3.7 million ha in Latin America, and 2.8 million ha in Africa.[2] Average grain yields of upland rice are generally less than 2000 kg ha^{-1} in most of the upland rice producing regions due to many environmental stresses and use of low inputs by farmers.[3] Although upland rice yields are relatively low as compared to lowland rice, however, it will continue to be an important crop in its growing regions due to the low cost of production and lack of irrigation facilities to grow lowland rice.

Originally, allelopathy was defined as the biochemical interactions between plants of all kinds including the microorganisms that are typically placed in the plant kingdom.[4] Since then, the term has undergone several changes over time, and it is now defined as any direct or indirect harmful or beneficial effect by one plant on another through the production of chemical compounds that escape into the environment.[5,6] The International Allelopathy Society[7] defined allelopathy as any process involving secondary metabolites produced by plants, algae, bacteria, and fungi that influences the growth and development of agricultural and biological systems. This definition considers all biochemical interactions between living systems, including plants, algae, bacteria, and fungi and their environment.[8] Willis[9] reported that the basic conditions necessary to demonstrate allelopathy in natural systems are i) a pattern of inhibition of one species or plant by another must be shown, ii) the putatively aggressive plant must produce a toxin, iii) there must be a mode of toxin release from the plant into the environment, iv) there must be toxin transport and/or accumulation in the environment, v) the afflicted plant must have some means of toxin uptake, and vi) the observed pattern of inhibition cannot be explained solely by physical factors or other biotic factors, especially competition and herbivory. However, Blum et al.[10] reported that no study has ever demonstrated all of these criteria.

In Brazilian Oxisols, upland rice yield under monoculture is significantly reduced after two or three years of consecutive planting on the same area and such reduction in yield is attributed to auto-allelopathy.[11] Fageria and Souza[12] also reported yield reduction of upland rice in the third year when grown in rotation with drybean on a Brazilian Oxisol. Even though allelopathy in rice grown under monoculture has been a subject of continued research for a decade,[13–16] but scientific literature on allelopathy in upland rice is scarce and scattered. One question is whether allelopathic effects of upland rice can be used in controlling weeds in crops grown in rotation with rice and also adopting some management practices that could reduce autotoxicity of this crop. This paper reviews the published literature on the problems of allelopathy and its control in upland rice and ways to improve upland rice yields and yields of other crops grown in rotation with upland rice.

RICE ALLELOCHEMICALS

The organic compounds involved in allelopathy are collectively called allelochemicals[16] and chemistry of these various allelochemical compounds in terrestrial ecosystems has been extensively reported.[17–19] These allelochemicals include simple phenolic acids, aliphatic acids, coumarins, terpenoids, lactones, tannins, flavonoids, alkaloids, cyanogenic glycosides, and glucosinolates. Phenolic acids have been identified in allelopathic rice germplasm[20] and have previously been described as allelochemicals.[10,19] Most are secondary metabolites released into the environment by leaching, volatilization or exudation from shoots and roots. Many compounds are degradation products released during decomposition of dead tissues. Once these chemicals are released into the immediate environment, they must accumulate in sufficient quantity to affect plants, persist for some period of time, or be constantly released in order to have lasting effects.[21] Abiotic (physical and chemical) and biotic (microbial) factors can influence the phytotoxicity of chemicals in terms of quality and quantity required to cause injury.[22] After entering the soil, allelochemicals encounter millions of soil microbes. The accumulation of chemicals at phytotoxic levels and their fate and persistence in soil are important determining factors for allelochemical interference. After entry into soil, all chemicals undergo processes such as retention, transport, and transformation, which, in turn, influences their phytotoxic levels.[23]

Observation of apparent allelopathy in rice has recently drawn great attention, and there is much interest in identification of the allochemicals.[15] Identification of the phytotoxic compounds responsible for allelopathy will allow efficient generation of more allelopathic cultivars through traditional breeding or biological based genetic alterations. Such cultivars could become important tools in the development of advanced integrated weed management strategies for rice, which would be less dependent on synthetic herbicides.[20] Various researchers have attempted to identify allelochemicals released from rice.[24,25] Rimando et al.[20] developed a bioactivity-guided isolation method with the objective of isolating the allelochemicals from rice. Identified compounds were azelaic acid, p-coumaric acid, 1H-indole-3-carboxaldehyde, 1H-indole-3-carboxylic acid, 1H-indole-5-carboxylic acid, and 1,2-benzenedicarboxylic acid bis (2-ethylhexyl) ester.

MECHANISMS OF ALLEOPATHY

The production of allelochemicals may be considered as a chemical defense mechanism that is under both genetic and environmental control.[26] For instance, herbivore attacks,[27] insect damage,[28,29] and reduced soil fertility[30–32] will generally increase the synthesis of these compounds by the plants. This has been partly explained by the balance between carbon (C) and nutrient availability.[33] In particular, N deficiency has been shown to strongly affect the synthesis of polyphenols,[34] because it will affect growth more than photosynthesis, and thus N deficiency allows more carbohydrates to be available for phenolic synthesis.

Allelopathy is mediated by many types of compounds with different sites and modes of biochemical action.[6] Several modes of action for allelochemicals are involved in the inhibition and modification of plant growth and development.[35] Zeng et al.[36] studied physiological and biochemical mechanism of allelopathy of secalonic acid F (SAF) in higher plants. These authors concluded that SAF may weaken the protective ability of plant tissues against membrane lipid peroxidation and damage the whole membrane system of plants, resulting in the ultrastructure destruction of chloroplasts and mitochondria. Cell ultrastructure destruction causes a reduction of photosynthesis and root activities and an increase in respiration. These abnormal physiological processes contribute to the inhibition of plant growth.

ALLELOPATHY AND WEED CONTROL

Weeds are one of the most important causes of yield losses in rice.[37] In the upland rice ecosystem, yield loss estimates from weed infestation have ranged from 30 to 100%.[38,39] Moreover, weeds increase production costs and lower rice quality. In major rice producing countries like India and China, hand weeding is the most common practice for weed control by small farmers. It is no doubt that hand weeding is a very efficient method of weed control but it is very laborious and time consuming. The time required for hand weeding varies from 45 to 455 d/ha, corresponding to 40 to 50% of the total labor input.[40] In all rice ecosystems, an increase in wage rates and labor shortage has led to a replacement of hand weeding with chemical control. This has created concern for environmental and health effects.[41,42] Consequently, there is need to identify sustainable weed management systems for rice production that will reduce the use of herbicides and the burden of hand weeding. Rice plants with allelopathic effects on weeds can mean lower production costs because the need for herbicide application and/or hand weeding is reduced. Thus, using rice cultivars having allelopathic properties or incorporating genes into rice cultivars that produce allelopathic compounds while maintaining grain yield and quality of subsequent crops could benefit farmers, consumers as well as the environment.[37] Liebman and Dyck[43] stated that including allelopathic plants in a crop rotation or as part of an intercropping system may provide a nonherbicide mechanism for weed control. They found few studies that focused on use of allelopathy in rotations, but management of allelopathic cover crops for weed control has been extensively investigated.[44] Results of those studies are directly applicable to crop rotations.[45]

Laboratory and field experiments have shown that rice allelopathy can suppress both monocot and dicot weeds.[13,24,38,46] Rice varietal differences in allelopathy and weed suppression have been reported.[16] Several accessions of rice germplasm in the field were found to decrease the growth of ducksalad [*Heteranthera limosa* (Sw.) wild.],[47] which is a major weed in the southern United States and causes a 21% reduction in the yields of direct-seeded rice.[48] In field experiments, some rice cultivars produced a weed free radius of 10 to 15 cm around an individual plant while other were densely surrounded by ducksalad. Rice cultivars with an allelopathic effect to barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] have been screened by assessment in the field and laboratory conditions.[13] Ebana et al.[49] studied the allelopathic effect of rice on lettuce (*Lactuca sativa* L.) and ducksalad with water-soluble extracts. Extracts from the leaves of rice seedlings at the six-leaf stage inhibited the growth of ducksalad and lettuce, and a close relationship existed between the inhibitory effect and the two test plants.

Chou and Lin[50] reported that aqueous extracts of decomposing rice residues in soil inhibited the root growth of rice and lettuce seedlings. Six phenolic acids (p-salicyclic, p-coumaric, vannilic, syringic, ferulic, and mandelic acid) with allelopathic properties were isolated from decomposing rice straw and paddy soil.[51] A total of 16 potential allelochemicals, including the above mentioned compounds have been found in rice.[13]

TRAITS ASSOCIATED WITH ALLELOPATHY IN RICE

Identifying traits associated with allelopathy is important in a breeding context. Allelopathic competition, being dependent of several physiological and phenological traits, and allelopathy are both polygenic characters.[16] Wu et al.[52] reviewed the possibilities of genetically improving crops with allelopathic potential and stated that allelopathy can play an important role in future weed management. To be able to breed for plant interference potential, it is important to know the genes coding for allelopathic potential and competitive ability generally. Before an efficient breeding strategy can be formulated, it is necessary to know which genes are involved in plant interference. Molecular marker-aided genetics is presently the best tool for studying the genetic control of a quantitative trait, mapping the genes involved on the chromosomes with a reasonable level of precision, and analyzing the relationships between the traits of interest and other important agronomic traits.[16]

Genetic study of allelopathy in rice was conducted at the International Rice Research Institute (IRRI), Philippines.[37] The crosses were made between IAC 165, a Brazilian highly allelopathic upland rice cultivar, and a cultivar C0 39, moderately allelopathic accession. Using this population, four quantitative trait loci (QTLs) have been identified that correlate with allelopathy expression, measured as barnyardgrass root reduction in laboratory screening.[37] This indicates that allelopathy is quantitatively inherited. A genetic study conducted by Dilday et al.[53] on the F_2 progeny from a cross between allelopathic rice accession PI312777 and rice cultivar Lemont and concluded that the allelopathic effect of rice on ducksalad was quantitatively inherited. Olofsdotter[16] has reported that a large proportions of Brazilian upland rice germplasms are allelopathic in nature. However, weed selectivity, autotoxicity, and residual effects from Brazilian rice germoplasm are different from those of Asian germoplasm.[16]

ALLELOPATHY AND ENVIRONMENT

Allelochemicals produced and released in the soil may pose environmental problems depending on the types of chemicals and their concentration. Once the phytotoxins are produced and escape into the environment, they begin to decompose either by microorganisms or by chemical action not involving microorganisms.[18] Whether allelochemicals can pollute ground water is practically unknown. To characterize their potential hazards, environmental studies are necessary.

CONTROL OF RICE AUTOTOXICITY OR ALLELOPATHY

When upland rice cultivars are planted on Oxisols of central Brazil for more than two years consecutively, rice yields decline significantly with time[12] and such yield reduction may be related to allelopathic residual effects or autotoxicity.[37] Similarly, experiments with rice in the Philippines have also shown the residual effects of allelochemicals on the reduction of yields of subsequent rice crops.[16] Chou[54] reported a 25% reduction in rice yield of a second crop in Taiwan and such reduction was attributed primarily to the phytotoxins produced during the decomposition of rice residues left on the soil. The phytotoxic effects of decomposing rice residues in the soil on the succeeding crop has been problem in some areas of the world[54] and autotoxicity is reported to explain the impossibility of growing two successive upland rice crops.[37] Understanding of these residual effects, including autotoxicity, is important in planning crop cycles or cropping systems. Crop management strategies to decrease the residual phytotoxic effects on succeeding crops need to be identified and studied further.[16]

Land which is degraded due to rice allelochemicals can be restored to normal productivity by adopting suitable management practices. These practices include improving soil organic matter content, keeping land fallow for a period of time wherever possible, using appropriate crop rotation, using the degraded land for pasture purposes, planting allopathic resistant cultivars and improving nutrient supply. A synthesis of information on the role of these management practices in control of allelopathy is given here. However, detailed discussion on influence of abiotic and biotic soil factors on phytotoxic levels of allelochemicals is given by Blum et al.,[10] Dalton,[55] Huang et al.,[56] Inderjit et al.,[57] Novak et al.,[58] Schmidt and Ley,[59] and Inderjit.[22]

IMPROVING SOIL ORGANIC MATTER CONTENT

Maintaining adequate level of organic matter in the soil is a useful method of neutralizing toxic chemicals produced in the process of allelopathy by plants. Soil organic matter content can be improved through application of animal manures and green manuring, use of crop rotation and adapting conservation tillage.

The beneficial effects of organic matter in detoxifying chemical substances depends on the concentration and the type of chemical compounds and also on other soil chemical properties. Soil organic matter may coat mineral surfaces (e.g., Mn^{2+}, Fe^{2+}), which prevents phenolic acids from directly contacting mineral ions and thus influencing the oxidation of phenolic acids. Cheng[60] suggested that oxidation of organic chemicals is not directly related to content of Mn^{2+} and Fe^{2+} in the soil but depends on the extent to which these inorganic ions are exposed to organic chemicals. Phenolic compounds are reported to be polymerized into humic acids by manganese (Mn), iron (Fe), aluminum (Al), and silicon (Si) oxides, however, Mn oxide is the most powerful catalyst.[56]

Fageria and Souza[12] conducted a field experiment growing upland rice and common bean in rotation on an Oxisol of central Brazil (Table 1). Data in Table 1 show that upland rice yield of the 3rd crop was significantly decreased when compared with 1st and 2nd crops even under high fertility treatments. However, medium soil fertility + green manure treatment maintained upland rice yield of 3rd crop compared with other fertility

Table 1. Response of Upland rice and common bean grown in rotation to chemical fertilizers and green manure on Brazilian oxisol.

	Grain yield kg ha^{-1}					
Fertility level[a]	1st Upland rice crop[b]	1st bean crop	2nd Upland rice crop[b]	2nd bean crop	3rd Upland rice crop	3rd bean crop
Low	2188a	1935b	2383a	866c	480c	890c
Medium	2428a	2382a	2795a	1831ab	1127b	1242ab
High	2330a	2568a	2657a	2432a	1324b	1486a
Medium + Green manure	—	2344a	—	1202bc	2403a	1065bc

Values followed by the same letter in the same column are statistically not different by the Tukeys test at the 5% probability level.
[a] Soil fertility levels for rice were low (without addition of fertilizers); medium (50 kg N ha^{-1}, 26 kg P ha^{-1}, 33 kg K ha^{-1}, 30 kg ha^{-1} fritted glass material as a source of micronutrients); high (all the nutrients were applied at the double the medium level). *Cajanus cajan L.* was used as a green manure at the rate of 25.6 t ha^{-1} green matter. For common bean the fertility levels were low (without addition of fertilizers); medium (35 kg N ha^{-1}, 44 kg P ha^{-1}, 42 kg K ha^{-1}, 30 kg ha^{-1} fritted glas material as a source of micronutrients) and high (all the nutrients were applied at the double the medium level).
[b] In the 1st and 3rd rice crop plots with medium + green manure fertility level were planted with green manure and incorporated about 90 days after sowing (at flowering) and hence grain yield was not presented.
Source: Fageria and Souza.[12]

treatments. However, green manure did not help in improving common bean grain yield. This means that organic matter supplied through green manure only helped to maintain upland rice yield.

KEEPING LAND FALLOW

Using fallow vegetation is a biological approach to regenerating the fertility of degraded soil.[61] During the fallow period, plant nutrients are taken up from various soil depths and stored in the fallow vegetation. The nutrients depleted during cropping are replenished with those from fallow vegetation. The litterfall from the fallow vegetation increases soil organic matter content. The groundcover by fallow vegetation enhances the soil biological activity. Replenishment of soil organic matter and regeneration of biological activity led to an increase in soil porosity and reduction in soil compaction.[61] This practice is only possible where land is available for such management and on such lands forage species can be grown for livestock feeding.

Kang et al.[62] suggested planting herbaceous or woody species to replace natural vegetation for soil regeneration. Advantages of planting woody fallow include efficient nutrient pumping out from the subsoil because of the deep rooting system, high biomass production, nutrient accumulation, and production of timber and fuel wood for income generation especially for farmers in developing countries.[63]

A fallow land system may improve activities of beneficial microorganisms in the soil. Temperature, moisture, and food supply are major components of the earthworm habitat.[64] With the return of cropped land to fallow land, the earthworms' habitat is improved because of lower soil temperature, higher soil moisture, and better food supply, leading to a potential increase in earthworm populations. Earthworms contribute to soil processes through fecal excretion (casts), burrowing, feeding, and digestion. Casts are nutrient rich and are an intimate mixture of soil, water, and microbial cells.[65] Earthworm burrows provide pathways for root exploration.[66] Earthworms are known to accelerate plant residue decomposition in the tropics and elsewhere[67] and play a role in converting plant residue into soil organic matter.[68–70] Tian et al.[61] reported that an increase in earthworm population on fallow land led to an increase in leaf litter decomposition, soil organic matter, available P, and extractable cations and pH; and a decrease in soil bulk density and penetrometer resistance in the fallow plots. Lal[71] also reported that eliminating earthworms led to high soil bulk density and unfavorable soil structure.

USE OF CROP ROTATION

Crop rotation or sequentially growing crops on the same land is an age-old practice in agriculture. Crop rotation is having many beneficial effects on crop growth such as control of diseases, insects and weeds, improving soil fertility and organic matter content, improving water use efficiency and thereby increasing crop yields. Further, such practice brings diversification and reduces the risk of economic loss to farmer. Crop rotation can improve overall soil quality which includes soil physical, chemical, and biological factors. Generally, a legume crop is preferred with cereals in the crop rotation scheme for maximum beneficial effects and best soil management practice. Guimares and Yokoyama[72] studied effects of upland rice–soybean rotation and upland rice planted in monoculture on Oxisol of Brazil (Table 2). Upland rice yield was significantly reduced in monoculture as compared to grown in rotation with soybean. This illustrates that the negative effects of rice allelopathy on the rice crop can be reduced by crop rotation. Similarly, Fageria[1] reported that substantially higher yield of upland rice can be obtained on an Oxisol when it is grown in rotation consisting of upland rice–common bean–corn–soybean (Table 3).

USE OF LAND FOR PASTURE

A part of the crop land can be used for pasture production in order to reduce the negative effects of allelochemicals produced by upland rice. For this purpose appropriate cropping systems should be adopted on the farm land to include crops and animal husbandry for sustainable crop production. Pasture improves soil quality through improving the organic matter content of the soil. In addition a large proportion of nutrients ingested by animals is

Table 2. Upland rice grain yield in rotation with soybean and grown in monoculture on a Brazilian oxisol.

Crop rotation	Grain yield ($kg\,ha^{-1}$)
Rice after three years of soybean	4325
Rice after one year of soybean	2577
Rice in monoculture for five years	1160

Source: Guimaraes and Yokoyama.[72]

Table 3. Grain yield of four crops grown in upland rice–dry bean–corn–soybean rotation on a Brazilian oxisol.

Crop rotation[a]	Grain yield ($kg\,ha^{-1}$)
First upland rice crop	4887
First dry bean crop after first upland rice crop	1674
First corn crop after first dry bean crop	8424
First soybean crop after first corn crop	1323
Second upland rice crop after first soybean crop	3982
Second dry bean crop after second upland rice crop	2152
Second corn crop after second soybean crop	8578
Second soybean crop after second corn crop	1560

[a] Rice and corn were planted during rainy season (November to March) and dry bean and soybean were planted during dry season (June to October) using sprinkler irrigation.
Source: Fageria.[1]

returned to the soil in the form of urine and feces.[73] Animals retain only a small proportion, about 20%, of the nutrient they ingest, and the rest is returned to the soil through excreta.[74] The expected buildup in soil fertility in a grass-legume pasture under grazing condition could result from a more rapid cycling and greater proportion of nutrients in a plant available form. Appropriate management of pasture land improves soil biological activity and reduces soil erosion. The increased biological activity is beneficial to the soil properties such as mineralization, humification, texture, porosity, water infiltration, and retention. Rao et al.[74] reported that the contribution of legume residues to soil organic matter quality and turnover together with improved soil fertility, soil structure, and biological activity were associated with a $1\,t\,ha^{-1}$ yield increase in a rice crop following 10-year-old grass + legume plots that did not require any N fertilizer when compared with rice following a grass-alone pasture of the same age.

PLANTING ALLELOCHEMICAL RESISTANT CULTIVARS

Planting allelochemically resistant cultivars of upland rice is an important strategy for improving yield of this crop on allelochemically degraded lands. Research has shown that rice cultivars have a wide range of variation in allelopathic activity.[16,49]

IMPROVING NUTRIENT SUPPLY

Adequate supply of nutrients in an appropriate proportion is an important aspects of growth and development of crop plants. Deficiencies of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and boron (B) have been reported to increase concentration of allelochemicals in the crop plants.[6] This means that plant residues of nutrient deficient plants incorporated in the soil or left in the field after harvest will have higher concentration of allelochemicals compared with plant residues supplied with adequate nutrients. It has been also reported that large amounts of allelochemical compounds were leached from the living intact roots, dried roots, and tops of phosphate deficient plants than from phosphate sufficient ones.[75] Phosphorus deficiency is one of the most important yield limiting nutrient for upland rice in Brazilian Oxisol.[76] Hence, P deficiency may aggravate allelopathy problem in upland rice grown on Brazilian Oxisols.

Further, it has been reported that allelopathic compounds inhibit mineral uptake due to alteration of cellular membrane functions of the plant roots.[77] Allelopathic compounds can depolarize the electrical potential difference across membranes, a primary driving force for active ion uptake. Allelochemicals can also decrease the ATP (Adenosine triphosphate) content of cells by inhibiting electron transport and oxidative phosphorylation, which are two functions of mitochondrial membranes. In addition, allelochemicals can alter the permeability of membranes to mineral ions.[77] The dominance of physiological mechanisms involved in inhibition of ions uptake by plant roots depend on type of allelochemicals, their concentrations and environmental conditions.

CONCLUSIONS

Rice crop grown on well-drained natural soils and which is totally dependent on rainfall for its water need is known as upland rice. The critical distinguishing characteristic of upland rice is that surface water accumulation does not occur for any significant period of time during the growth season. Yield of upland rice is low however, due to the low cost of production this system of rice culture will continue to have an important role in crop production in various regions of the world. Significant yield reduction of rice has been observed if it is grown in monoculture on the same land for more than 3 years. Allelochemical effects are considered as one of the main reasons for such yield decline.

In many situations, allelochemicals entering the soil undergo chemical, physical, and biological degradation. These changes often limit the accumulation of allelochemicals at phytotoxic levels. Phytotoxicity of allelochemicals depends on their concentration, movement, fate, and persistence in the soil. Allelochemical effects can be reduced by adopting certain management practices. These practices include using the crop rotation, improving organic matter content of the soil, and leaving cropped areas fallow for certain periods of time to allow decomposition of allelochemicals, planting resistant cultivars and improving nutrient supply. There is a large variation in allelopathy among rice cultivars. More research is needed to understand the effects of soil and crop management practices on the availability and rate of degradation of allelochemicals.

Promising results in rice allelopathy research offer the possibility to use this phenomenon in breeding programs to enhance weed control in upland rice. Additionally, developing allelochemically resistant cultivars is also important strategy for improving upland rice yield on allelochemically degraded soils. To incorporate the allelopathic trait in improved rice varieties destined for uplands, a reliable screening technique along with an understanding of the trait variability and genetic control is desired. Allelopathic potential has been demonstrated in rice and screening techniques are available to test for the allelopathic potential of cultivars against important weed species, although knowledge of the mechanisms of action is still meager.

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