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REVIEW

Rice allelopathy and its properties of molecular ecology

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Abstract Crop allelopathy is a promising and environmentally friendly method in weed control; however, the inducible genetic trait for allelopathy in the suppression of weeds needs to be overcome for practical use. Further study needs to be directed to this end to elucidate the molecular genetics and its physiologic mechanism. In this paper, the authors review recent advances in the investigation of rice allelopathy and its molecular regulatory mechanism, especially in responses to stressful conditions including biotic and abiotic factors in China. Previous studies show that rice allelopathy could be enhanced when the rice accession was exposed to stressful conditions, and further analysis by the transcriptomics and proteomics approaches conducted in our laboratory indicated that the increase in allelopathic potential of rice, when exposed to the stresses, was attributed to increased expression level of genes involved in phenolic synthetic metabolism. The increasing phenolic compounds have been confirmed as the main allelochemicals and they jointly act to suppress the target, especially in responses to stressful condition, but it seems to be the primary effect in phenolic allelopathy. We still wonder how the exudates from rice root, which were released into rhizosphere soil, are transformed by soil microorganism to produce the higher secondary effect of phenolic allelopathy in the suppression of weeds. Therefore, the authors suggest that rhizosphere biologic properties of allelopathy in rice and its mechanism are being the key research areas in the world now, and systems biology and its approaches, such as metagenomics and metaproteomics, would be helpful to reveal the process and its molecular ecological mechanism regarding rhizospheric biology of rice allelopathy.

Keywords Allelopathy, rice, molecular mechanism, stress

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1 Introduction

Rice (*Oryza sativa* L.) is a staple crop for billions of people worldwide, but its production is often constrained by uncontrolled weeds, which might cause 45%–95% loss in yield (Moody, 1991; Lin et al., 2000). This problem was traditionally tackled by extensive use of chemical herbicides. However, the increased herbicide resistance in weeds and concerns about harmful environmental effects of herbicides have put pressure on farmers to reduce their use. It is essential to find sustainable and environmentally acceptable alternative weed management methods. The allelopathy fits the requirements in weed control, and it has drawn increasing attention.

Allelopathy is a characteristic biologic phenomenon in some plants, algae, bacteria, coral and fungi. The organisms with allelopathic potential can release certain secondary compounds, called allelochemicals, to impact the growth and development of neighboring organisms. Rice (1984) in his monograph on allelopathy enlarged the definition to include all direct positive or negative effects of a plant on another plant or on microorganisms by the liberation of the compounds into the environment. The relevant studies on rice allelopathy began about 20 years ago in the United States. Dilday et al. (1991) first reported on rice allelopathy. Since then, several groups around the world have been working on screening rice cultivars for allelopathic potential in order to evaluate the possibilities for utilizing allelopathic features in rice to securely control weed. In China, there were many ancient records about allelopathic phenomena in literature, and it has been a new research focus especially in rice since the last decade of the 20th century (He et al., 2005; Lin et al., 2006; Shen et al., 2008). This paper reviews the findings on rice allelopathy and its molecular ecological properties, and discusses the current challenges, opportunities and future direction in the investigation of rice allelopathy.

2 Performance in rice allelopathy

A rice plant with allelopathic potential is referred to as the "donor plant," while the "receiver plant" is the target of the allelochemicals released from the donor plant, such as the accompanying barnyardgrass with the allelopathic rice (He et al., 2006, 2009). Laboratory bioassay is the first step in investigating the possible involvement of allelopathy (Foy, 1999). Many bioassays have been designed and used to detect allelopathic potential in rice germplasm. Since the same rice cultivar may respond differently with different screening bioassays, ideal bioassays should be conducted with samples directly from the target plants (receiver) naturally occurring or cultivated adjacent to presumed allelopathic plants (donor); meanwhile the appropriate screening bioassay in laboratory should be convenient, reliable, cost-effective and universal.

Our previous studies showed that the relay seeding in agar (RSA) (Navarez and Olofsdotter, 1996; Jensen et al., 2001) provided a rapid, simple and inexpensive approach to screen rice accessions with allelopathic potential against a target weed under laboratory conditions. The RSA method shows the highest efficiency in the evaluation of allelopathic potential when it was compared with relay seeding in silica (RSS) and seeding in rice root-exudation (SRE) methods (Shen et al., 2004). The result obtained from the evaluation by different bioassays of eight rice accessions showed that the mean inhibitory rate of eight rice accessions in the suppression of target weed, barnyardgrass, by RSA, was significantly increased by 86.4% and 91.3%, compared to that by SRE and RSS, respectively. But no differences were found in the case by SRE and RSS. The eight rice cultivars possessed higher inhibitory rate (IR) on the target weed by RSA than that by SRE and RSS. However, their inhibitory rates varied by SRE and RSS. PI312777, IAC47 and IAC120 demonstrated higher inhibition by SRE and RSS. And the reverse was true in other accessions, indicating that the same rice cultivar showed marked differences in inhibitory rate by SRE and RSS. It was therefore suggested that RSA was the best bioassay method, by which the result could truly represent the performance of allelopathic potential in each entry (Table 1).

In this method, the pregerminated donor plants were grown for seven days in two rows on agar in the Petri dish, and barnyardgrass was then relay-seeded between the two rows of receiver plants. The roots of the donor plants on the agar medium could fully interact with the receiver plants. Allelochemicals released from the roots of the donor plants were diffused into the agar medium to affect the root growth of the receiver plants. The lengths of the receiver plant roots were then used to indicate allelopathic activity of the donor plant. The continuous growth of the donor plant seedlings ensured a constant release and accumulation of allelochemicals into the agar medium, which was almost similar to the continuous growth in nature.

Table 1 IRs of rice cultivars tested with three methods and their significant comparison

rice accessions	inhibitory rate			
	RSA	SRE	RSS	average
PI312777	57.2	43.2	35.4	45.0abA
Lemont	10.8	−33.4	4.2	−6.0eD
Moroberekan	23.4	14.6	17.6	18.4dC
IAC25	50.0	35.1	45.0	43.6abA
IAC47	45.3	35.9	21.0	34.1bcAB
IAC120	46.9	42.6	17.3	24.4cdBC
Batatais	47.5	13.5	35.8	35.9abAB
Iguape Cateto	58.2	38.2	42.1	46.2aA
Average	44.0aA	23.6bB	23.0bB	30.2

*The data in this table are averages of three replications. The small letter indicates a significant difference at the 5% level, whereas the capital letter shows a significant difference at the 1% level. IR: inhibitory rate.

We used this method (RSA) to successfully evaluate the allelopathic potential of more than 300 rice accessions with different allelopathic potential in the suppression of barnyardgrass. Five rice cultivars such as Iguape Cateto, PI312777, Azucena, Taichung Native1 and IAC25 showed over 50% IR on barnyardgrass root growth, and IR was expressed as inhibition rate on the root length of barnyardgrass; it was transformed by $[\mathrm{IR} = (1 - \mathrm{TR}/\mathrm{CK}) \times 100\%]$, where TR represents the treatment and CK refers to the control. IRs of 12 cultivars, such as AU257, Red Rice5, IAC164 and Mafeng1, ranged from 40% to 50%. IRs of 21 cultivars including Taizhung 189, Dinorado, Arroz decampos, and Shuangzhan 2 ranged from 30% to 40%. IRs of 13 cultivars, such as Fengaizhan, IR721413, IR60080-46A, and IR72412, ranged from 20% to 30%, while IRs of the remainder cultivars, such as Zhengyou 1, IR55423-01, Pratao Precoce, Aisanruzhan, Muxiang 25 and Lemont, were less than 20%. The results showed that the number of rice accessions under different allelopathic potentials fit well to normal distribution, implying that only 1%–3% of rice germplasm in the collected accessions showed strongly allelopathic potential in the suppression of the target weeds.

As the genetic variability of the allelopathy is widespread in the collected rice accessions, it is essential to investigate the underlying genetic diversity of them. The analysis of ISSR by our group (He et al., 2004) showed that the rice accessions with higher allelopathic potential could be clustered into different groups, and some of the higher allelopathic rice accessions introduced from the same geographical locations can be grouped into the same sort, such as rice accessions IAC25, IAC47 and IAC120 from Brazil; however, the others from different geographical locations were also clustered in the same group, such as PI312777 and Taichung Native 1 introduced from America and Taiwan of China, implying that the genes conferring allelopathy in those rice accessions might be allelic or non-allelic. This finding suggested that rice allelopathic potential can be increased through the recombination of the non-allelic genes in rice breeding. However, most of rice accessions with different allelopathic abilities in the same group, such as Iguape Cateto (strong allelopathy), Dourado Pecoce, Pratao Precoce and Lemont (non allelopathy), exhibited lower genetic polymorphism in terms of allelopathic effect on the target plants. This might be attributed to oriented selection for the desirable traits including high yielding, good quality and strong resistance in rice breeding program, in which the wild types of the rice entries might once have possessed high allelopathic activity, and this character inadvertently attenuated through continuous selection of rice plants for other desirable characteristics (Putnam and Duke, 1974).

3 The inherence of rice allelopathy and its properties of genetic ecology

Rice allelopathy was characterized by quantitative traits, which was controlled by polygenes (Dilday et al., 1998, 2000; He et al., 2004). Therefore, the expression of genes associated with allelopathy in rice might be mediated by external environment including the developmental phases. So it is very crucial to examine the developmental genetic characteristics of allelopathy in the rice seedling stage to provide basic information for selection and breeding of allelopathic rice in higher suppression of weeds. For this purpose, the specific study was conducted in our lab (Dong, 2002; Lin et al., 2003). The additive-dominance genetic model and its statistical method, including the quantitative traits of the interaction between genotype and environment at the specific developmental stage ($0 \rightarrow t$) and in the given developmental phase ($t\text{-}1 \rightarrow t$), were used to study the developmental inherence of allelopathy in rice at seedling stage (Zhu, 1995). Five parental rice varieties with different allelopathic potentials were employed in diallel cross $\{P(P+1)/2\}$ to get a set of genetic materials including parental lines and two generations of F_1. The results showed that conditional additive and dominant effects expressed alternatively from 3- to 8-leaf stages of rice seedlings, which is the key period to prevent weed infestation in rice production. The additive effects were significant in the 5|4, 6|5, and 8|7-leaf phases, whilst the dominance effects appeared to play an important role in the 4|3 and 7|6 leaf phases. The conditional narrow sense heritability was significant in the 5|4, 6|5, and 8|7 leaf phases, and the broad sense heritability was pronounced among all the growth periods investigated, suggesting that selection for allelopathic activity should be performed during this three leaf phases in order to improve selection response (He et al., 2004).

Since rice allelopathy was characterized by quantitative inherence, quantitative trait locus (QTLs) analysis could be chosen as the principal method for the genetic improvement and molecular breeding of allelopathice rice. So far only seven studies have been reported on mapping QTLs for allelopathy in rice (Xiong et al., 2007a). Ebana et al. (2001) reported a study from an F2 population derived from the cross between an indica type line PI312777 (highly allelopathic) and a japonica cultivar Rexmont (less allelopathic). Seven QTLs were identified on chromosomes 1, 3, 5, 6, 7, 11 and 12. A multiple QTL model estimated that five QTLs with a LOD score higher than 3.0 collectively accounted for 36.6% of the total phenotypic variation. The second study was done using a population of 142 recombinant inbred lines (RILs) derived from a cross between cultivar IAC 165 (japonica upland variety) and cultivar CO39 (indica irrigated variety). Four main-effect QTLs located on three chromosomes were identified that collectively explained 35% of the total phenotypic variation of the allelopathic activity in the population (Jensen et al., 2001). The other studies were documented by Zeng et al. (2003), Xu et al. (2003), and Lee et al. (2005) independently. However, the common aim of those studies was to determine the QTLs associated with allelopathy in suppression of target plants. None of the studies actually was aimed to determine simultaneously the epistatic loci effects and their interactions with the environment using their own established genetic maps for rice. As with most other genetic traits, rice allelopathy is a quantitative trait strongly mediated by environmental conditions. This restricts the efficiency and progress in breeding for higher levels of allelopathic potential. In fact, the significance of genotype × environment (GE) interactions in the genetic control of quantitative traits has long been recognized by quantitative geneticists. Because of the GE interaction, QTLs that are important in one environment may not be as important as in another environment in determining the phenotype (Xiong et al., 2007a). For this reason, QTL with little GE interaction across a set of environments would be desirable in marker-assisted breeding program. Therefore, we focused on new QTL development and its interactions (including digenic epistatic effects and their environmental interactions) using RSA bioassay (Shen et al., 2004) and the mixed linear statistic model developed by Zhu (1995). More recently, we have established a mapping population of 123 F_{10} lines (RILs) derived from a cross between Japonica variety, Lemont (non-allelopathice rice) and Indica variety, Dular (allopathic rice). The QTL analysis was done for allelopathy in the rice varieties during 2004 and 2005. IR on the root length of the target plant barnyardgrass (*Echinochloa crus-galli*) was detected in a RIL population of rice accessions by using RSA bioassay method. The two QTLs that had significant additive effects on the root length of target plant barnyardgrass were identified and mapped to chromosomes 2 and 5, which performed 3.69 and 3.05 LOD values and explained 6.95% and 4.35% of phenotypic variance, respectively, of which one locus performed its significant interaction with environment (AE). Epistasis analysis indicated that there were three pairs of QTLs in the marker intervals located on chromosomes 1, 3, 4, 5 and 10, performing significant additive × additive interactions for allelopathic effects on the root length of receiver plant barnyardgrass with positive epistatic effects, of which one pair of loci was significant in additive × additive interactions with environment (AAE). The findings suggested that a "favorable" gene with positive additive effects might become "unfavorable (deleterious)" following transfer into a new variety due to the large negative additive × additive effects in the new genetic background. Therefore for rice allelopathy, QTL mapping and selection experiments should place more emphasis on identifying the best multi-locus allelic combinations instead of pyramiding individual favorable QTL alleles. The previous results also showed that using MAS would not eliminate genotype × environment interactions for allelopathy in rice. Epistatic effects between QTLs were also found to be important, suggesting that combinations of QTLs for allelopathy need to be selected for, rather than selection of individual QTLs. Due to the complications of genotype × environment interaction and epistatic effects, it is therefore suggested that phenotypic selection might be as effective as marker-assisted selection (MAS) (Paterson et al., 1991) for the germplasm and environments that are evaluated (Xiong et al., 2007a).

4 The enhancement of rice allelopathy and its regulatory mechanism in the response to stressful conditions

Previous studies showed that crop allelopathy in the suppression of weeds, which was characterized by quantitative inheritance, could be significantly regulated by environmental conditions including biotic and abiotic factors (Einhellig 1999; Wu et al., 1999; Belz, 2007). The investigation by our group has been certified that rice allelopathy can be markedly enhanced when allelopathic rice accession was exposed to stressful conditions including low fertilizer supplies and dry or wet-seeding conditions, etc (Shen and Lin, 2007; Xiong et al., 2007b; Wang et al., 2007, 2009a, 2009b; Song et al., 2008; Sun et al., 2009b).

To explore the inducible mechanism of weed-suppressive potential in allelopathic rice accession mediated by external environmental conditions, we studied the molecular physiological properties of allelopathic rice regulated by different fertilizer supplies in hydroponics using real-time fluorescence quantitative PCR (qRT-PCR). We found that in hydroponics, the weed-suppressive potential of allelopathic rice PI312777 was enhanced under low fertilizer supplies including low nitrogen, phosphorus and potassium treatments, respectively, showing higher inhibitory effects on the dry weight of barnyardgrass in the presence of root exudates of allelopathic rice PI312777 than control (normal nutrient condition). However, the reverse was true in non-allelopathic rice Lemont. qRT-PCR analysis showed that the expressions of all the nine enzymatic genes involved in phenolic synthesis were increased by 2.3–6.0 fold in the leaves and by 1.9–5.4 fold in the roots of allelopathic rice, PI312777, respectively with the exception of two genes encoding CoA-ligase and salicylate glucosyl transferase, showing 1.7 and 2.3 fold down-regulations in the leaves of the allelopathic rice accessions, respectively, when exposed to the lower nitrogen supply. However, in the non-allelopathic rice (Lemont), the expressions of these genes were mostly down-regulated from 1.4 to 3.5 times in the roots and from 1.2 to 4.0 times in the leaves, with the exception of cinnamoyl alcohol dehydrogenases up-regulated by 1.5 fold in the leaves, phenylalanine ammonia-lyase (PAL) and cinnamoyl-CoA up-regulated by 1.0 and 1.4 fold respectively in the roots. High performance liquid chromatography (HPLC) analysis confirmed that allelopathic rice had an increased exudation of phenolic compounds when supplied with lower nitrogen, resulting in an elevated allelopathic activity, while little change happened in non-allelopathic rice. Further analysis suggested that the nutrient-stressed conditions might induce the synthesis of signal molecules such as salicylic acid (SA) and then trigger a cascade of systemic chemical defense reactions through up-regulated expressions of relevant genes involved in phenylpropanoid metabolism pathway because of decreased demand for proteins required for rice growth when exposed to low nitrogen supply. In this process, ammonium ions released by PAL can be assimilated to increase N cycling compensating for nitrogen deficiency. The resulting N-free carbon skeletons of t-cinnamate can be shunted into phenylpropanoid metabolism. Simultaneously, the differential expression of the key genes controlling isoprenoid metabolism in PI312777 and Lemont was investigated under lower nitrogen supply levels. The results indicated that 12 detected key enzyme genes, which are involved in isoprenoid synthesis in rice plants, were mediated by lower nitrogen level. Of the 12 genes, six were up-regulated, and the others were down-regulated in allelopathic rice PI312777. The similar tendency was also found in its counterpart Lemont, showing that out of 12 tested genes, six up-regulated genes and five down-regulated genes detected in PI312777 were also found in Lemont. In other words, 11 out of 12 key genes involved in isoprenoid metabolic pathway in the two rice accessions had the same gene expression patterns under low nitrogen condition compared with the controls. The result strongly suggested that the related genes involved in isoprenoid metabolic pathway possessed the same or similar molecular ecological behavior in response to the changes of nutrient supplies in the molecular scale (Wang et al., 2007; Xiong et al., 2007b). This in turn resulted in increased production of phenolic compounds. Phenolic acids have been identified in allelopathic rice germplasm (Rimando et al., 2001) and they have previously been described as allelochemicals, especially in stressful condition (Rice, 1987; Chou et al., 1991; Inderjit, 1996; Blum, 1998; Mattice et al., 1998, 2001; Kim et al., 2000; Lin et al., 2001; Seal et al., 2004; Yang et al., 2004; Berendji et al., 2008). It is therefore suggested that the increase of phenolic acids results in enhancement of allelopathic potential in rice when exposed to lower nitrogen supply. In others words, phenolic acids as allelochemicals played a key role in rice allelopathy, especially in environmental stress. The result has been further confirmed in our lab by using proteomic approach (Xiong, 2008; Sun, 2009a).

Rice allelopathy is a chemoecological process through which the rice plant exerts a harmful influence on its neighboring target weed by the release of chemical compounds into environment via volatilization, leaching, excretion and decomposition. As mentioned above, allelopathic rice could release phenolic acids into soil to inhibit the accompanying weed, especially, when the rice is under stress, such as nitrogen, phosphorus, potassium, and water deficiencies, as well as higher density of barnyardgrass. However, whether phenolic acid allelochemicals give an advantage or a disadvantage to soil ecological system still remains a controversial issue. Nevertheless, investigating the fate of allelochemicals in the soil and demonstrating how phenolic acids influence the physical, chemical and biological characteristics of the soil are very helpful for understanding the mechanism of rice allelopathy in the field. Accordingly, we employed five phenolic acids such as p-hydroxybenzonic acid, ferulic acid, vanillic acids, SA, and cinnamic acid, which have been identified in the exudates of rice, as exogenous allelochemicals to evaluate the impact of phenolic acids on soil microorganism and nutrient availability. The result indicated that the added phenolic acids had a positive effect on microbial flora and enzyme activity in soil, suggesting that applying rice allelopathy in weed control is a promising and environmentally friendly method. Yet, it still needs more work to analyze the diversity of microorganisms in the soil mediated by the phenolic acids to further understand how the added phenolic compounds impact the rhizosphere biological process of allelopathic rice in the soil ecosystem.

5 Rhizosphere biology of rice allelopathy

It has been noticed that most of the rice cultivars exhibit an inhibitory effect on weeds in the laboratory; however, this effect becomes insignificant in the field trial. It is yet unknown whether this phenomenon is caused by the antagonistic effect from rhizospheric microbes in the field, or the loss of allelopathic compounds in the soil. Studying the characteristics of the rhizospheric soil microflora can assist in understanding the rhizospheric biological process of the rice allelopathic function, and meanwhile revealing the chemical ecology of the allelopathic process. Up to now, very limited research has been conducted in this field. Therefore, we conducted a study to investigate the dynamics of microbial populations and their functional diversities in the seedling rhizosphere soils of rice cultivars with varied allelopathic activities by employing agar plate bioassay, fumigation and BIOLOG analysis (Lin et al., 2007). The result showed that rice cultivars significantly affected the microbial carbon content in their associated rhizospheric soil. The microbial carbon contents were ranked in a decreasing order as Iguape Cateto ($441.0\ \mathrm{mg \cdot kg^{-1}}$) > IAC47 ($389.7\ \mathrm{mg \cdot kg^{-1}}$) > PI312777 ($333.2\ \mathrm{mg \cdot kg^{-1}}$) > Lemont ($283.8\ \mathrm{mg \cdot kg^{-1}}$) with the nil-rice control soil of $129.3\ \mathrm{mg \cdot kg^{-1}}$. Similarly, the respiration rate of the soils was 1.404, 1.019, 0.671 and $0.488\ \mathrm{gC \cdot g^{-1} \cdot h^{-1}}$ for PI312777, Iguape Cateto, IAC47 and Lemont, respectively. The respiration rate was only $0.304\ \mathrm{gC \cdot g^{-1} \cdot h^{-1}}$ for the control soil. The microbial flora in the rhizospheric soil of different rice cultivars was dominated by bacteria (58.4%–65.6%), followed by actinomycete (32.2%–39.4%) and fungi (2.2%–2.8%). BIOLOG analysis showed that the value of Average Well Color Development (AWCD) differed significantly among rice cultivars. It was always the highest in the rhizospheric soil of the strongly allelopathic rice cv. PI312777, and the lowest in the rhizospheric soil of the poorly allelopathic rice cv. Lemont. The AWCD value reached the maximum in all the sampled soils after 144 h of incubation. The AWCD values from the rhizospheric soils of PI312777, IAC47, Iguape Cateto and Lemont were 1.89, 1.79, 1.60 and 1.43 times higher than that of the control soil. Principal component analysis (PCA) identified three principal component factors (PCF) in relation to carbon sources, accounting for 70.1%, 11.3% and 7.0% of the variation, respectively. Nineteen categories of carbon sources were significantly positively correlated to the three principal components. Phenolic acids, carbohydrates, amino acids and amides were significantly correlated to principal component 1, phenolic acids, carbohydrates and fatty acids to principal component 2, and carbohydrates and hydroxylic acids to principal component 3. Amino acids and amides were the two main carbon sources separating the three principal component factors. In addition, the total microbial population in the rhizospheric soil was significantly positively correlated with AWCD, microbial biomass carbon, microbial respiration and Shannon index. There was a significantly positive correlation between the total microbial population and the IR on the root length of lettuce owing to the different allelopathic activities of the rice cultivars. These results suggest that changes in microbial population, activity and functional diversity in the rhizospheres are highly cultivar-dependent. These changes might play an important role in governing the rice allelopathic activity in the field. However, as the limitations of the culture methods become clear, many different techniques for evaluating microbial communities have been developed in order to enable modern microbiologists to understand natural microbial community structure and dynamics. Recently, many technologies have been used to explain the diversity of soil microorganisms from molecular level, such as terminal restriction fragment length polymorphism (T-RFLP) (Park et al., 2006; Bennett et al., 2008; Euringer and Lueders, 2008), denaturing gradient gel electrophoresis (DGGE) (Hong et al., 2007; Hu et al., 2007; Ying et al., 2008), and single-strand conformation polymorphism (SSCP) (Smalla et al., 2007; Schmalenberger et al., 2008). These approaches are a culture-independent fingerprinting technique, by which it is expected to overcome the weakness that culturing approaches show us only the tip of the iceberg in regard to the genetic diversity and complexity of soil microbial communities. Therefore, more recently, we have used T-RFLP to analyze and compare the differences in the diversity of microorganisms in the rhizosphere of allelopathic rice PI312777 and its counterpart Lemont under low nitrogen condition. The result showed that some microorganisms functioning in nitrogen cycle, nitrification, nitrogen fixation and producing exotoxin, were significantly increased in the rhizosphere of PI312777 compared with those in the rhizosphere of its counterpart, which contribute to enhance tolerance in nutrient limited condition via the regulatory machinery to enhance nitrogen utilization efficiency and allelopathic effect in the suppression of the target weed. The huge following challenge is annotating the microbial diversity with functional details in microbial ecosystems mediated by the allelochemicals. For this purpose, we have attempted to use transcriptomics to decipher gene expression in the soil microbial systems mediated by allelopathic rice accession, especially in the exposure to stressful conditions, but the transcriptomics is still limited in its application to understanding of protein abundances, and thus cellular and community function, with the reason that mRNA abundance is not always related to protein abundance, and post-translational modifications cannot be currently predicted by mRNA (Gygi et al., 1999; Griffin et al., 2002; Nie et al., 2006). Proteins play the primary role in carrying out cellular functions encoded by the genome, so the large-scale study of protein abundances in soil should provide a significant leap to get insight into the understanding of the soil ecological processes and the environmental factors that govern microbial activity and survival (Taylor and Williams, 2010). So elucidating the changing properties in the expression abundance of soil proteins is an effective way to understand the function of soil microorganisms in the response to environmental factors, such as the allelochemicals released from the allelopathic rice accessions. More recently, we have developed an effective sequential extraction and separation method to extract the protein from different agricultural soil samples and in turn to separate the proteins by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) or two-dimensional gel electrophoresis (2-DE), which could be successfully used for the large scale study of soil metaproteomics using mass-spectrometric technique combined with bioinformatics. MALDI-TOF/TOF analysis by our group indicated that the proteins from allelopathic rice soils function in xenobiotic detoxification, conversion of allelochemicals, chemotaxis and signal transduction, etc. These results suggested that the function of soil proteins mediated by the allelochemicals is complex and further work needs to deeply examine the metaproteome change and their function in rhizosphere soil of allelopathic rice.

6 Summary and prospects

Rice being the most important food crop in the world has the possibility to take the lead in this new scientific challenge. The investigation of allelopathy shows that it is promising to use allelopathic activity against weed in sustainable agriculture systems. Rice allelopathy has been confirmed as an inducible genetic trait (Bi et al., 2007) that is associated with molecular regulation of secondary metabolic pathways (Bi et al., 2007; Song et al., 2008; Fang et al., 2009). Therefore, it might be feasible to trigger allelopathic potential through alteration of agricultural practice or manipulation of environmental conditions. Further study needs to be directed to this end to elucidate the molecular genetics and enzymology of the metabolic pathways associated with the biosynthesis and liberation of allelochemicals, and to establish a series of specific management strategies that can be applied to crop production to avoid down-regulation of the relevant genes associated with allelopathic activity (Belz, 2007; Macías et al., 2007; Fang et al., 2009).

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