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Edited by:

Vijai Bhadauria

Crop Development Centre/Dept. of Plant Sciences
51 Campus Drive
University of Saskatchewan
Saskatoon, SK S7N 5A8 Canada.
Tel: (306) 966-8380 (Office), (306) 716-9863 (Cell)
Email: vijai.bhadauria@usask.ca

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Current Status of Proteomic Studies on Defense Responses in Rice

Xifeng Chen[1], Vijai Bhadauria[2] and Bojun Ma[1]*

[1]College of Chemistry and Life Sciences, Zhejiang Normal University, Jinhua, 321004, China
[2]Crop Development Centre/Dept. of Plant Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5A8 Canada
*Corresponding author: E-mail: mbj@zjnu.cn;
Tel.: 86-579-82282949; Fax: 86-579-82282269
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Abstract
Biotic stresses are constraints to plant growth and development negatively impacting crop production. To counter such stresses, plants have developed stress-specific adaptations as well as simultaneous responses. The efficacy and magnitude of inducible adaptive responses are dependent on activation of signaling pathways and intracellular networks by modulating expression, or abundance, and/or post-translational modification of proteins associated with defense mechanisms. Proteomics plays an important role in elucidating plant defense mechanisms by mining the differential regulation of proteins to various biotic stresses. Rice, one of the most widely cultivated food crops in world, is constantly challenged by a variety of biotic stresses, and high-throughput proteomics approaches have been employed to unravel the molecular mechanism of the biotic stresses-response in rice. In this review, we summarize the latest advances of proteomic studies on defense responses and discuss the potential relevance of the proteins identified by proteomic means in rice defense mechanism. Furthermore, we provide perspective for proteomics in unraveling the molecular mechanism of rice immunity.

Introduction

Plants often suffer from biotic stresses caused by various pathogens, such as fungi, bacteria and viruses, which lead to significant damage, and even death. In evolution, plants have developed effective defense mechanisms to cope with various pathogenic microorganisms encountered at almost every stage of their development. In the process of defense response, plants regulate the expression of related intracellular resistance proteins to adjust their physiological state or morphology to resistant and inhibit the invasive pathogens. Many proteins are subjected to modifications at their C- or N-termini following synthesis, and various types of post-translational modification (PTM) play an important role in the plant defense signaling network. Therefore, the search for resistance-related proteins may significantly improve our understanding of plant defense mechanisms, which, in turn, will help to design rational strategies to improve plant disease resistance.

High-throughput proteomics studies can provide information in quantitative protein profiling, dynamic PTM, protein subcellular localization/compartmentalization, dissection of signaling pathways and protein-protein interactions (Agrawal et al., 2011; Agrawal et al., 2013; Hossain et al., 2012; Matros et al., 2011). In current high-throughput proteomics, plant proteins are classically separated on the two-dimensional electrophoresis (2-DE) gel, and followed by mass spectrometry (MS) or tandem MS (MS/MS) or liquid chromatography (LC)-MS/MS (Rakwal and Agrawal, 2003). Many plant species have been used to study quantitative changes in protein abundance in response to different abiotic and biotic stresses (Fang et al., 2015; Hu et al., 2015). Proteomic data have been used to determine the quantitative and qualitative changes in related proteins in plants and to understand the relationship between these proteins and biological processes. Hence, plant proteomics not only can identify the proteins involved in the direct defense responses but also can reveal the relationships between defense responses and biological processes, in which the identified proteins participating.

Rice is a seminal model plant of monocotyledons species and is the one of the most widely cultivated food crops throughout the world. Rice development and production is constrained by the diseases caused by various fungal, bacterial, and viral pathogens (Gnanamanickam et al., 1999). Proteomics studies in rice has made considerable progress in providing functional information of proteins under various physiological conditions in the various developmental stages, tissues, cells, and abiotic and biotic stress environments (Komatsu and Tanaka, 2005). In this review, we summarize the recent advances in rice proteomic studies on defense responses and discuss the potential relevance of the proteins identified by proteomic means in rice defense mechanism.

Proteins identified by proteomic approaches that are responsive to various pathogens

1. Fungi

Defense response of rice to the fungal pathogens like *Magnaporthe oryzae*, *Rhizoctonia solani* and *Cochliobolus miyabeanus*, have been investigated by proteomic studies. Rice blast, caused by *M. oryzae*, is one of the most destructive diseases of rice. Using the combined approaches of 2-DE and MS, Kim *et al. (*2004) identified 8 proteins including receptor-like protein kinases (RLK), β-1,3-glucanase, peroxidase, probenazole-inducible protein (PBZ1), and pathogenesis-related protein (PR5, PR10), induced by *M. oryzae* in rice inoculated leaves, all of which are defense-related. Li *et al. (*2015) conducted a time-course phosphoproteomic analysis on the leaves of both

resistant and susceptible rice cultivars infected with *M. oryzae*, and 56 phosphoproteins belonging to 12 functional categories have been identified by MS/MS. The defense-related proteins, defense signaling-related proteins, and microtubule-associated proteins are differentially phosphorylated between the compatible and incompatible interactions, and such differences apparently contributed to the difference in resistance against fungal infection in the two cultivars (Li et al., 2015). However, the proteins involved in photosynthesis, antioxidation, and protein folding were not differentially accumulated between the resistant and the susceptible cultivars. These proteins could substantially enhance reactive oxygen species (ROS) production and contribute to the basal resistance of the plant against the pathogens (Li et al., 2015).

Sheath blight, caused by the fungus *R. solani*, is another major fungal disease of rice world-wide. Lee et al. (2006) used 2-DE and ESI Q-TOF MS to identify proteins upregulated in resistant and susceptible rice in response to *R. solani*. Six proteins identified with presumed anti-fungal (β-1,3-glucanase), photosynthetic (RuBisCO) and proteolytic (proteasome) activities were increased in both susceptible and resistant plants, suggesting a common baseline defense response for different host-pathogen interactions; An additional 8 proteins with anti-fungal activity (3-β-hydroxysteriod dehydrogenase, 3-β HSD; chitinase), glycolysis (glyceraldehyde 3-phosphate dehydrogenase, GAPDH), and anti-oxidation (ascorbate peroxidase, APX) were increased only in the resistant line (Lee et al., 2006). The induction of 3-β HSD was detected for the first time in resistant rice plants in response to pathogen challenge, suggesting a defensive role of this enzyme in rice against *R. solani*. (Lee et al., 2006).

Fungus *C. miyabeanus* causes brown spot disease in rice leaves resulting in yield loss. To understand the interaction between rice and *C. miyabeanus*, Kim et al. (2014) employed proteomic approaches of 2DE and nESI (nano-electrospray ionization)-LC-MS/MS in the *C. miyabeanus*-infected rice leaves, and successfully identified the sequences of 63 protein spots (39 increased and 24 decreased). In response to *C. miyabeanus*, the levels of enzymes involved in Calvin cycle (fructose bisphosphate aldolase; sedoheptulose-1, 7-bisphosphatase; RuBisCO; transketolase, TKL) and glycolysis (phosphoglycerate kinase; enolase; GAPDH) decreased in rice leaves, whereas the levels of enzymes in the TCA cycle (oxaloacetate; aspartate aminotransferase), ethylene biosynthesis (homocysteine S-methyltransferase), antioxidant process (APX; superoxide dismutase, SOD; peroxiredoxin, PRDX) and PR proteins (β-1,3-glucanase; PR5; PR10; salt induced protein, SalT) increased in rice leaves (Kim et al., 2014).

2. Bacteria

Current proteomic studies of rice defense responses against bacterial pathogens mainly focus on *Xanthomonas oryzae pv. oryzae* (*Xoo*), which is the second most important rice pathogen causing bacterial blight. Using 2-DE and MS, Yu *et al. (*2008) identified 64 differentially regulated proteins proteins from rice leaves infected with *Xoo*, and these proteins were those with various functions in photosynthesis (RuBisCO; oxygen-evolving enhancer protein, OEE), protein turnover (translational elongation factor; proteasome), glycolysis (GAPDH) and antioxidant defense (APX; glutathione S-transferase, GST), *etc*. Interestingly, 51 of these 64 proteins were involved in photosynthesis. Notably, the reduction in the level of larger fragment of RuBisCO large subunit (RcbL) was concomitant with increasing in the level of smaller fragments of RcbL, indicating that intact RcbL are degraded following *Xoo* attack (Yu et al., 2008).

Mahmood et al. (2006) analyzed the proteome of plasma membrane (PM) and cytosol from rice leaves inoculated with compatible and incompatible races of *Xoo*, respectively, and identified 20 differentially expressed proteins in response to *Xoo*, in which 9 were induced and 10 were depressed by compatible race, while 7 were induced and 3 were depressed by incompatible race. These proteins were related to photosynthesis (RuBisCO; OEE; ATP synthase, chloroplast), metabolism (TKL; GADPH) and defense (PR5; PBZ1; SOD; PRDX). Interestingly, RcbL was also found to be fragmented into two smaller proteins upon infections by two different *Xoo* races (Mahmood et al., 2006).

By using an improved method of PM protein purification, Chen *et al. (*2007) conducted PM proteomics of the rice suspension cells expressing a disease resistance gene *Xa21*, to identify PM components involved in the early defense response to bacterial blight. Eleven protein spots with predicted functions in plant defense were identified by MS/MS, including H^+-ATPase, phosphatase, hypersensitive-induced response protein, prohibitin, zinc finger protein, universal stress protein, and heat shock protein (HSP), demonstrating that direct proteomics analysis of rice PM can be applied to identify potential PM components involved in the rice defense response to microbes (Chen et al., 2007).

3. Virus

Despite large number of studies on viral diseases to date, the knowledge of the proteins that control viral diseases is limited. The rice yellow mottle virus (RYMV) is a member of the *Sobemovirus* genera, and destructive for rice production (Pinel et al., 2000). The RYMV is considered as a model virus to study the molecular mechanisms of viral resistance (Sire and Brugidou, 2002). Using 2-DE and LC-MS/MS, Ventelon-Debout *et al. (*2004) identified 32 differentially regulated proteins involved in metabolism, defense, and translation in the rice cells infected by RYMV, and these proteins belonged to three functional categories: defense/stress-related proteins, metabolism, and translation and protein turnover. A number of proteins regulated by abiotic stress response pathway (such as PR10, HSP, SOD, SalT, Dehydrin, Ethylene-inducible protein) were activated by RYMV in rice leaves, and proteins involved in glycolysis pathway such as phosphoglycerate mutase, phosphoglycerate dehydrogenase, aldolase C1 and GADPH were also detected during RYMV infection, suggesting that the glycolysis

pathway plays an important role in defense/stress response.

Unlike fungi or bacteria, viruses generally encode a significantly smaller set of proteins, *e.g.* RYMV with only four open reading frames (Siré, 2002). It is likely that the virus recruits host proteins to finish their life cycle and cope with host defenses. To prove these multiple interactions, Brizard et al. (2006) extracted the protein complexes formed in the infected rice leaves by RYMV, and identified a large number of proteins from the complexes by MS. The proteins identified in the complexes are those involved in plant defense, metabolism, translation, protein synthesis and intracellular transport, presumably important for viral replication and movement. Surprisingly, no viral proteins were identified in the complex, indicating that viruses are able to recruit various host proteins with different functions to fulfill their life cycle (Brizard et al., 2006).

4. Elicitor

Fungal pathogens often release oligosaccharides, known as the elicitors, that can be specifically recognized by receptors on the host plasma membrane and this specific recognitions can trigger intracellular immune responses (Basse et al., 1993). Kim *et al. (*2003) discovered elicitor-induced 14 proteins in rice cells cultured in a suspension containing crude extracts of the rice blast fungus, and most were PR proteins including PBZ1, PR10, Isoflavone reductase (IRL) and SalT. Agrawal et al. (2002) revealed that proteins APX, PR5 and PR10 were accumulated in rice leaves treated with chitosan, a major component of many fungal cell walls, and demonstrated that chitosan triggers defense-signaling pathways in leaves of rice. Liao et al. (2009) used CSB I, an elicitor purified from fungus *M. grisea*, to treat rice leaves, and detected the differentially expressed proteins by 2-DE and LTQ (linear ion trap)-MS/MS. The identified proteins were functionally classified into defense proteins (PR10a, PR5 and SalT), ROS metabolites enzymes (SOD, GST and CAT), cell death related (translationally controlled tumor protein), signal transduction, molecule biosynthesis and metabolism categories (Liao et al., 2009). Commonly, these proteins were induced faster and stronger in incompatible interactions than compatible ones (Kim et al., 2003; Kim et al., 2009; Liao et al., 2009).

5. Lesion mimic mutants

Lesion mimic mutant (LMM) plants spontaneously display necrotic lesion on leaves without any pathogenic infection (Lorrain et al., 2003). The phenotype of LMM is similar to hypersensitive response (HR), which is a form of programmed cell death (PCD) associated with resistance to pathogens through rapid induction of local cell death around the infection site (Morel and Dangl, 1997). Most LMMs constitutively activate immune responses, including deposition of callose, induction of *PR* genes, production of ROS and accumulation of phytoalexins (Staskawicz et al., 1995), and display enhanced resistance to pathogens, such as rice blast and/or bacterial blight (Mizobuchi et al., 2002; Wu et al., 2008). Therefore, LMMs constitutes a powerful tool to unravel the pathways of PCD and disease response in plants.

Recently, the comparative proteomics between wild type (WT) rice and LMMs of *cdr1* (cell death and resistance; Takahashi et al., 2003), *cdr2* (Tsunezuka et al., 2005), *blm* (blast lesion mimic; Jung et al., 2006), *spl1* (spotted leaf; Kim et al., 2008) and *spl6* (Kang et al., 2007) have been reported. We also analyzed the proteomics of a rice LMM of *spl5* (Chen et al., 2013). These proteomic results showed that proteins involved in ROS scavenging, defense responses or cell death, such as SOD (*spl1*, *blm*), CAT (*spl6*, *blm*), Peroxidase (*spl1*), APX (*spl5*, *blm*), GST (*cdr2*, *spl5*), were induced in LMMs, whereas proteins involved in photosynthesis and glycolysis, such as RuBisCO (*spl1*, *spl5*, *spl6*, *blm*, *crd2*) and GAPDH (*spl1*, *spl5*, *cdr2*), were often depressed in LMMs. As expected, defense-related protein like PR5 (*spl1*), PR10 (*blm*), PBZ1 (*spl1*, *cdr2*, *blm*) and Chia2a (*spl5*) were significantly over-accumulated in LMMs. These results suggest that the decreased photosynthesis and energy metabolism were coupled with the increased oxidative stress and defense responses in LMMs, which might be a common feature for PCD or defense response in plant (Jung et al., 2006).

Proteomics-based identification of the factors in rice immunity

Plant makes a transition from growth and reproductive posture to a defensive posture, must undergo a global up- and down-expression of genes in defense response (Bilgin et al., 2010). Most proteins identified in rice by the proteomic approaches in response to different pathogens are those abundance of PR proteins (fungus, Kim et al., 2004; bacterial, Mahmood et al., 2006; virus, Ventelon-Debout et al., 2004) and ROS-related proteins (fungus, Kim et al., 2014; bacterial, Yu et al., 2008; virus, Ventelon-Debout et al., 2004), reflecting the general roles rather than a specific role in response to a specific pathogen. These results just confirmed the previously known conclusions drawn from using traditional approaches and are therefore not particularly useful in identifying new factors or unraveling new pathways in rice immunity. Identification of the low abundance proteins with critical roles in rice immunity is usually hampered by both the presence of these high abundance "noise" proteins and the limited sensitivities of the available proteomic methodologies (Wagner et al., 2002). Despite these limitations, some biologically meaningful information has been extracted from these proteomic studies in rice. Firstly, it has been shown for the first time that 3-β HSD with anti-fungal activity was induced only in resistant rice plants in response to *R. solani*, suggesting a defensive role of this enzyme in rice against *R. solani*. (Lee et al., 2006); secondly, the protein complex formed in response to RYMV infection in rice cells contains no viral proteins but only the host proteins presumably required for the viral life cycle (Brizard et al., 2006); thirdly, the rice RcbL was found to be fragmented upon *Xoo* infections seemingly in a race-independent manner (Mahmood et al., 2006; Yu et al., 2008). This may be possibly explained by the observation that ROS induces fragmentation of the RuBisCO protein *in vitro* (Ishida et al., 1999; Ishida et al., 1997). However, the functional role of RcbL fragmentation in rice immunity remained to be determined; lastly, the photosynthesis and

energy metabolism are attenuated in favor of the enhanced oxidative and defense responses in different LMM mutants (Chen et al., 2013; Jung et al., 2006; Kim et al., 2008; Tsunezuka et al., 2005), which might be a common feature for PCD or plant immunity.

At present, besides the aforementioned fragmented information, little systematical new information has been obtained in rice immunity using high through-put proteomic approaches. This largely due to the limited proteomic data generated so far. With the saturation of the rice proteomic data of rice-pathogen interactions (both compatible and incompatible interactions) at different stages of the entire infection processes, new protein factors or enzymes involved in different stages of rice immunity including those in pathogen recognition, signal transduction initiated or exerted through protein-protein interactions/protein modifications/degradations, transcriptome reprogramming and production/biosynthesis of metabolites with anti-pathogen activities or cell wall strengthening will be eventually identified. Proteomic studies in rice, especially in defense response or immunity are still at its rudimentary stage. Adequate data are required to draw a clear picture of rice immunity. However, given the complex nature of the proteomic data, challenges remain even with the saturated dataset available. The ability to extract the biologically meaningful information from the hierarchy massive dataset and the ability to distinguish the primary casual events from the interference of the secondary consequent events are critical to dissect rice immunity pathways or networks. The application of combinatory approaches of functional genomics, proteomics, and metabolomics will certainly be helpful in speeding up this identification process.

Concluding remarks and prospects

High through-put proteomic studies are playing increasingly important roles in deciphering virtually every aspect of cellular functions in plant stress responses, as well as in establishing possible relationships between protein abundance/modification and plant stress tolerance. However, many challenges remain in proteomic studies. One of the constant challenges for proteomics is inadequate protein identification because of the interference of high abundance proteins (Wagner et al., 2002). For example, RuBisCO consists of 30 to 50% of total plant protein from green tissues, and causes less analytical sensitivity and dynamic range in protein identification of plant proteomics (Krishnan and Natarajan, 2009; Rose et al., 2004; Widjaja et al., 2009). This challenge can be resolved with the removal of the abundant proteins from proteomic samples and increasing the sensitivities of proteomic detections for the low abundant proteins. The application of the newly developed advanced methodologies such as gel-free protein separation approaches, multidimensional protein identification technology, quantitative proteomic approaches including isotope-coded affinity tags, targeted mass tags, and isobaric tags for relative and absolute quantitation will certainly help to resolve this problem. Another challenge is how to translate the massive data of proteomics from different researches into knowledge, which can interpret the pathway and/or network mechanism in plants and be readily applied into crop improvement programs. The solution might largely hinge on developing interdisciplinary approaches, creating sufficient genetic resources, and establishing robust bioinformatics tools with novel algorithmic solutions. In that case, with the saturation of proteomic data, the potential biomarkers in the linear pathways or intertwined networks common or unique to each biotic stress will be revealed, and these biomarkers will be useful for generating the next-generation crop plants using molecular breeding and/or coupled with genetic engineering with enhanced crop yield and seed quality.

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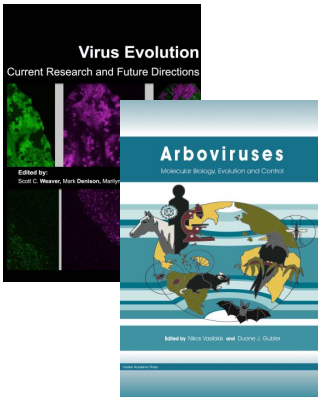

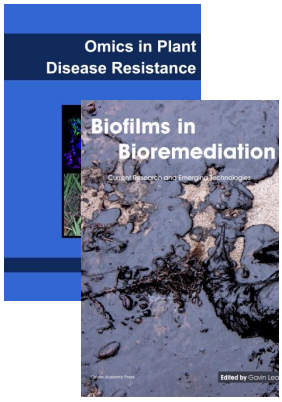

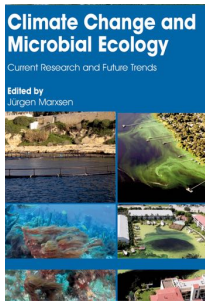

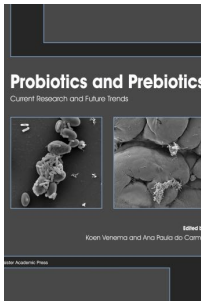

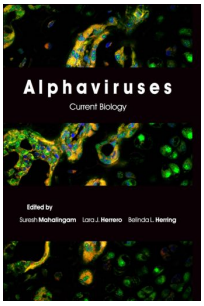

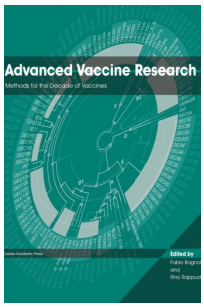

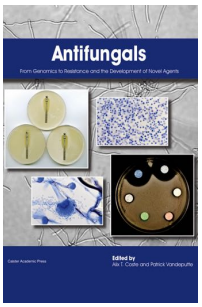

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