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Comparative proteomic analysis of rice stripe virus (RSV)-resistant and -susceptible rice cultivars

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Abstract

Rice stripe disease is one of the most devastating and widespread rice viral diseases caused by rice stripe virus (RSV). Some rice cultivars have been shown to be resistant to RSV; however, the proteins and genes responsible for the resistance are rarely characterized. To explore this resistance mechanism, in this study we employed proteomic tools including two-dimensional electrophoresis (2-DE) and mass spectrometry (MS) to globally identify differential proteins between a RSV-resistant rice cultivar Xudao 3 (*O. sativa* L. spp. *japonica*, cv. Xudao 3) and a RSV-susceptible rice cultivar Wuyujing 3 (*O. sativa* L. spp. *japonica*, cv. Wuyujing 3). Our data showed that 27 proteins were statistically different during the three-leaf stage of seedlings between Xudao 3 and Wuyujing 3. 15 of them were up-regulated and the other 12 proteins were down-regulated in Wuyujing 3. 20 differential proteins were successfully identified through mass spectrometry and database search. Interestingly, some proteins related to stress and/or defense responses were down-regulated in Wuyujing 3, such as heat shock protein, protein disulfide isomerase, glyoxalase and Os04g0435700, which may be implicated in its susceptibility to RSV. Together, our work for the first time successfully identified some differential proteins related to RSV-resistance or susceptibility, providing candidate proteins and genes for subsequent investigations of their roles in rice resistance against RSV.

Keyword: 2-DE, MALDI-TOF MS, Proteome, Rice stripe disease, Rice.
Abbreviations: ACN: acetonitrile; 2-DE: two dimensional electrophoresis; CBB: coomassie brilliant blue; IEF: isoelectric focusing; MALDI-TOF MS: matrix-assisted laser desorption/ionization time of flight mass spectrometry; SDS-PAGE: sodium dodecyl sulphate polyacrylamide gel electrophoresis.

Introduction

Rice (*Oryza sativa* L.) is one of important food crops and provides the staple food source for half of the world population (Khush 2005; Sasaki and Burr 2000). Rice is suffering from various pathogens, such as rice stripe virus (RSV), which causes rice stripe disease and is one of the most serious and widespread rice viral diseases in the temperate regions of East Asia (Zhang et al., 2011). Interestingly, some rice cultivars are resistant to the infection of RSV. Moreover, four dominant resistance genes against RSV (*Stv-a*, *Stv-b*, *Stvb-i* and *RSV1*) have been mapped (Hayano-Saito et al., 2000; Hayano-Saito et al., 1998; Washio et al., 1968a; b; Zhao et al., 2010) and some QTLs associated with the resistance have also been located (Ding et al., 2005; Maeda et al., 2004; Sun et al., 2007; Wu et al., 2009), suggesting that rice does have certain resistance mechanism against RSV. However, the true identities of these genes and QTLs remain unknown, as well as their roles in rice resistance to RSV. Currently, it is also not known whether other rice genes or proteins are involved in RSV-resistance, and systematic studies are required to further explore the mechanism of rice resistance to RSV.

The proteomic approach is a well-established strategy to globally analyze protein expression profiles under various conditions (Agrawal et al., 2006; Agrawal and Rakwal 2011; Fan et al., 2011; Yang et al., 2007a; Yang et al., 2007b; Yang et al., 2006). It is successfully used to identify differential proteins related to different stresses or virus infections (Chi et al., 2010; Chitteti and Peng 2007; Ding et al., 2012; Fan et al., 2011; Nwugo and Huerta 2011; Torabi et al., 2009; Ventelon-Debout et al., 2004). It has also been observed that a number of proteins regulated by abiotic stress were triggered by virus infection (Ventelon-Debout et al., 2004), such as heat shock protein 70, ethylene-inducible protein, chaperonin 60. To explore the mechanism of rice resistance to RSV, in present work we used proteomic tools to identify differential proteins between RSV-resistant and -susceptible rice cultivars and try to find the candidate proteins and genes for subsequent investigations of their roles in rice resistance against RSV.

Results and Discussion

Protein expression profiles and differentially expressed proteins between Xudao 3 and Wuyujing 3

The proteomic tools 2-DE and MS are most widely used to identify differential proteins in rice (Chi et al., 2010; Chitteti and Peng 2007; Ding et al., 2012; Fan et al., 2011; He et al., 2011; Nwugo and Huerta 2011; Torabi et al., 2009; Yang et al., 2007a; Yang et al., 2007b; Yang et al., 2006), and are also used in present work. To improve resolution and accuracy, we firstly optimized the sample preparation, loading quantity, IEF parameters and CBB staining methods, as illustrated in Supplementary Fig. S1. In all, at least 798

protein spots could be detected on the 2-DE gels with a pH range of 4-7 and a mass weight range of 20-100 kDa, and most of the protein spots were distributed near the center region of the gels (Fig. 1). 97 differentially expressed proteins between Xudao 3 and Wuyujing 3 (ratios $_{\text{Xudao 3/ Wuyujing 3}} \geq 1.5$ or ratios $_{\text{Xudao 3/ Wuyujing 3}} \leq 0.67$) were detected using ImageMaster 2D Platinum software, and 27 protein spots were significantly different ($P < 0.05$) as analyzed by Statistical Package for the Social Sciences (SPSS) software.

MALDI-TOF MS identification of differentially expressed proteins and functional categorization

Among the 27 differentially expressed proteins, 20 protein spots were successfully identified through mass spectrometry and database search, as shown in Table 1. As for the other seven protein spots, no significant matches were found. There are two reasons for their absence: (1) the abundances of these proteins are very low (Fig. 1); and (2) the proteins may not be included in the databases. Moreover, three differential proteins had a MSCOT score less than 64, but their sequence coverage was 73%, 50%, and 32%, respectively, which strongly argued for their positive identification. Some protein spots were quite different from their expected molar mass and pI values, including spot 10, 14, 15, 16, 17, and 18. It is commonly found in proteomic studies, and is probably due to post-translational modifications, protein splicing or degradation (Jiang et al., 2007; Minagawa et al., 2008; Yan et al., 2006). According to Bevan et al. (1998), these 20 differential proteins can be divided into the following 6 categories: energy-related proteins, metabolism-related proteins, defense-related proteins, photosynthesis-related protein, molecular chaperone and unknown function proteins (Fig. 2).

We also identified some proteins related to stress and/or defense responses, including heat shock protein, protein disulfide isomerase, glyoxalase and Os04g0435700. Heat shock protein 70 (HSP70) (Fig. 3, spot 1) and protein disulfide isomerase (PDI) (Fig. 3, spot 3), the stress-related proteins, were down-regulated in Wuyujing 3. Heat-shock proteins (HSPs) play crucial roles in protein folding and implicated in various stress responses, such as osmotic stress, electric shock, pathogen attack, and so on (Li and Srivastava 2004; Singla-Pareek et al., 2003). HSP70 (Fig. 3, spot 1) has been observed to change during the *Rice yellow mottle virus* infection on rice, which indicated that HSP70 might share specific roles during virus infection (Ventelon-Debout et al., 2004). Protein disulfide isomerase (PDI) is a multifunctional protein and plays important role in protein folding process (Gilbert 2001). PDI is an essential folding catalyst which catalyzes disulfide formation and isomerization and a chaperone that inhibits aggregation (Wilkinson and Gilbert 2004). Furthermore, two defense-associated proteins were also identified to be down-regulated in Wuyujing 3 (Fig. 3, spot 7 and 8), which were glyoxalase and Os04g0435700 (similar to UVB-resistance protein UVR8). The glyoxalase is an enzyme responsible for the conversion of methylglyoxal to lactic acid and is widely distributed in plants, animal tissues, and microorganisms. (Unpublished data) Compared with Xudao 3, Zhendao 88, and Yandao 8 (RSV-resistant cultivars), these four proteins were similarly down-regulated in Wuyunjing 7 and Nipponbare (RSV-susceptible cultivars) (Fig. S2, spot 1 and 3; Fig. S3, spot 7; Fig. S4, spot 8). Of course, in present study using near-isogenic lines or mutants might be more persuasive. However, in present work we successfully identified 20 differential proteins from Xudao 3 and Wuyujing3, and 4 proteins related to stress and/or defense responses were also identified, suggesting their possible involvement in rice resistance against RSV. Therefore, to some extent, our work not only provides candidate proteins and genes for subsequent studies but also suggests proteomic approach may be useful to identify novel proteins or genes in rice studies.

Bioinformatic analysis of differentially expressed proteins

GO analysis showed that 16 different proteins were found with more than one matched GO numbers, 2 proteins with only one matched GO, while no GO annotations were available for number 9 and 14 protein spots. Most of the differentially expressed proteins were involved in cellular component, binding, catalytic, electron carrier, transporter, biological regulation, cellular process, establishment of localization, localization, metabolic process and pigmentation (Fig. 4). Interestingly, some of them showed function specificity, such as some down-regulated proteins in Wuyujing 3 that were only involved in the electron carrier, biological regulation and pigmentation (Fig. 4). This Go analysis provided us with good clues for subsequent studies of physiological roles of these proteins.

Materials and methods

Rice materials

Xudao 3 (*O. sativa* L. spp. *japonica*, cv. Xudao 3; highly resistant to RSV) and Wuyujing 3 (*O. sativa* L. spp. *japonica*, cv. Wuyujing 3; highly susceptible to RSV) were provided by Institute of Food Crops, Jiangsu Academy of Agricultural Sciences, China. Xudao 3 and Wuyujing 3 were registered by the Crop Cultivar Registration Committees of Jiangsu Province in 2003 and 1992, respectively, and were widely planted in Jiangsu Province. It is well demonstrated that RSV-resistant cultivars, such as Xudao 3, Zhendao 88, and Yandao 8, carry the *Stv-b*^{i} gene, while RSV-susceptibe cultivars, such as Wuyujing 3, Wuyujing 7, and Nipponbare, do not contain any *Stv-b*^{i} gene (Wang et al., 2009; Yao et al., 2009).

The culture condition

Rice seeds were surface sterilized for 30 min with 1% NaClO, washed 5 times using sterilized water, and soaked for 36 h in sterilized water at 28 °C, then germinated for 48 h in dark condition. Rice was cultivated in artificial climate chamber at 16 h light period (2000-2200 lux) and 8 h dark period. The culture temperature was within a range of 28°C-25°C. The leaves were collected at three-leaf stage seedling. Samples were frozen in liquid nitrogen immediately, and stored at -80°C.

Protein extraction

Protein extraction was performed using a modified protocol according to Shen et al (Shen et al., 2003). 0.2 gram samples were ground into fine powder in liquid nitrogen and homogenized on ice for 5 min in pre-cooled extraction buffer (20 mM Tris-HCl pH 7.5, 250 mM sucrose, 10 mM EGTA, 1 mM PMSF, 1 mM DTT, and 1% Triton X-100). The homogenate was transferred into an eppendorf tube and centrifuged at 15000 g, 4°C for 20 min. Then the supernate

Table 1. Differentially expressed proteins identified by MALDI-TOF MS.

Spot No.	Theoretical *M*r (kDa)/p*I*	MOWSE score	NMP [a]	Description	Function	SC [b]	Changed folds [c]	Accession No.
Down-regulated proteins								
1	67.68/4.97	233	20	Heat shock cognate 70 kDa protein	Heat shock protein /Molecular chaperone	51%	2.2	ABA95501
2	63.14/5.40	145	13	K01835 phosphoglucomutase	Metabolism	25%	1.8	NP_001051066
3	57.03/4.97	102	10	Protein disulfide isomerase	Protein quality /Molecular chaperone	25%	2.2	EAY80280
4	53.98/5.38	236	22	ATP synthase CF1 beta subunit	Energy	58%	2.8	YP_052756
5	54.04/5.47	207	18	ATP synthase CF1 beta subunit	Energy	54%	3.3	NP_039390
6	39.41/5.51	109	8	Glutamine synthetase	Metabolism	48%	1.6	NP_001048045
7	32.40/5.82	131	14	Putative glyoxalase I	Disease/defense	48%	4.3	BAD28547
8	48.66/5.37	169	14	Os04g0435700/Similar to UVB-resistance protein UVR8	Disease/defense	39%	2.0	NP_001052849
9	52.59/5.42	182	14	Hypothetical protein OsI_33814	Unknown function	44%	1.8	EAY78710
10	41.81/6.07	95	8	Fructose-bisphosphate aldolase	Metabolism	30%	2.1	ABA91631
Up-regulated proteins								
11	55.20/5.95	94	9	ATPase alpha subunit	Energy	24%	1.7	AAM12499
12	54.02/5.38	103	12	ATP synthase beta subunit	Energy	26%	4.1	BAA90397
13	52.39/5.59	191	17	RuBisCO activase small isoform precursor	Photosynthesis	47%	1.6	AAX95414
14	6.57/9.68	41	2	Hypothetical protein	Unknown function	73%	2.5	BAD19944
15	45.50/9.02	194	15	Photosystem II stability/assembly factor HCF136	Photosynthesis	53%	1.7	Q5Z5A8
16	41.27/7.28	86	7	mRNA-binding protein	Transcription	23%	1.9	NP_001059177
17	31.35/7.0	89	7	Hypothetical protein OsI_15938	Unknown function	37%	1.7	EAY94163
18	7.71/5.24	38	2	Hypothetical protein	Unknown function	50%	1.6	BAD87267
19	40.78/5.92	56	6	Putative transcription factor X1	Transcription	22%	1.7	BAD52538
20	15.27/5.03	135	7	ATP synthase CF1 epsilon subunit	Energy	84%	1.6	NP_039389

[a] Number of matched peptides.
[b] Sequence coverage.
[c] $P < 0.05$.

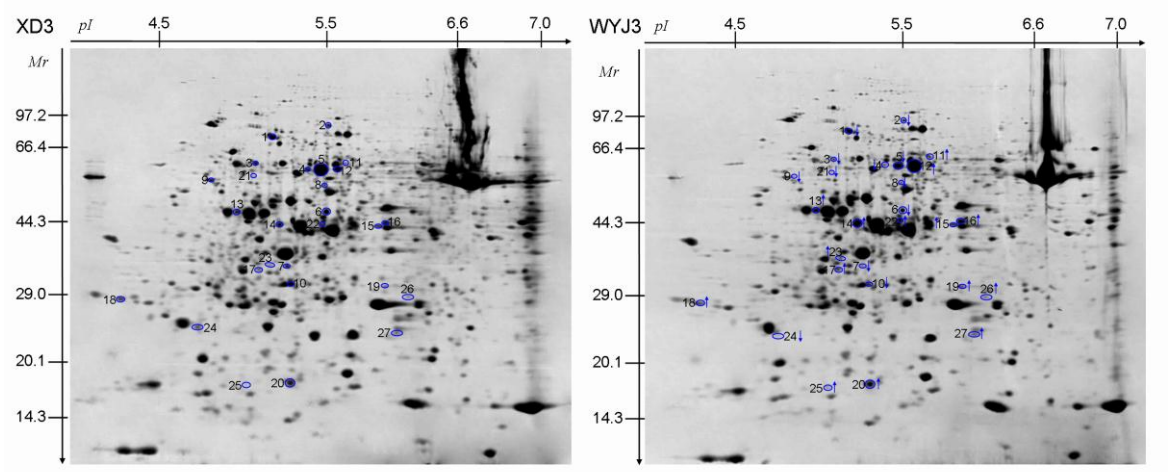

Fig 1. The proteomic profiles of Xudao 3 and Wuyujing 3. The protein spots (1~20) have been identified by MALDI-TOF MS. The upward and downward arrows respectively indicated up-regulated and down-regulated proteins. XD3, Xudao 3. WYJ3, Wuyujing 3.

was collected and protein was deposited using 1/4 volume 50% cold TCA in an icy bath for 30 min. After centrifugation (20min, 15000 g, 4°C), the supernate was discarded. The precipitate was washed four times with ice-cold acetone containing 0.07% (w/v) DTT, centrifuged (10min, 15000 g, 4°C/each time), and vacuum-dried. The dried powder was dissolved in sample buffer (7 M urea, 2 M thoiurea, 4%w/v CHAPS, 2% Ampholine, pH 3.5-10, 1% w/v DTT; 1 mg dried powder for 0.1 ml buffer) through vibrating at room temperature for 20 min, then overnight at 4 °C. Finally, the mixtures were centrifuged at 15000 g for 10 min at 4 °C and the supernate was used for two-dimensional electrophoresis. The protein concentration was determined by Bradford method (Bradford 1976).

2-DE

2-DE was carried out according to the manufacturer's protocol (GE Healthcare, BIO-Science). 400 μg Proteins were loaded onto immobilized IPG gel strip (GE Healthcare, BIO-Science) in the 4-7 pH range with 11 cm for passive rehydration (12~13 h). Then IEF was performed at 300, 500, 1000 V, and 8000 V for 1 h, respectively, and then remained 8000 V until a total voltage of 32000 Vh. Subsequently, the strips were equilibrated in equilibration buffer (0.05 M Tris-HCl pH 6.8, 2.5% SDS, 30% v/v glycerol and 1% DTT) for 15 min, and then equilibrated for 15 min again with the same equilibration buffer except that DTT was replaced with 2.5% w/v iodoacetamide. The second dimension SDS-PAGE was carried out and a Laemmli buffer system (Laemmli 1970) was used with 5% stacking gels and 15% resolving gels. Finally, the gels were stained with 0.1% CBB R-250 (0.1% CBB, 25% v/v ethanol, and 8% acetic acid).

Image and data analysis

The 2-DE gels were scanned using a UMAX Power Look 2100XL scanner (Maxium Tech, Taiwan, China). The image analysis was performed using ImageMaster 2D-platinum version 5.0 software (GE Healthcare BIO-Science). The optimized parameters were as follows: saliency = 2, smooth = 3, and minimum area = 50. Spots were normalized as a percentage of the total volume over the whole set of gel spots. Data were analyzed using SPSS software. The protein spots that passed the Student's *t*-test ($P < 0.05$) were considered to be differential proteins.

In-gel digestion and MALDI-TOF MS identification

Protein spots were manually cut down from the gels and rinsed in distilled water. The gels were destained 2~3 times by ultrasonic with 50 μl destaining buffer (25 mM NH_4HCO_3, 50% ACN) until the gels became colorless. Then, the gel pieces were cleaned using 25 mM NH_4HCO_3, 50% ACN, and 100% ACN, respectively, and vacuum-dried. The dried gel pieces were socked in 25 mM NH_4HCO_3 with 10 μg/ml of trypsin (Promega, Madison, WI, USA) at 4 °C for 30 min. Next, 10-15 μl 25 mM NH4HCO3 was added to the gel pieces and the digestion was allowed to proceed at 37 °C overnight (11-16 h). After digestion, the protein peptides were collected and subjected to MALDI-TOF MS (Bruker daltonics, Ultraflex-TOF-TOF, Germany). All the acquired peptide mass finger prints were analyzed online in the National Center for Biotechnology Information nonredundant database (NCBInr) through the Mascot program (http://www.matrixscience.com). *O. sativa* was selected as the taxonomic category. To determine the confidence of the identification results, the search parameters were set as follows: trypsin was selected as enzyme, one missed cleavage was allowed, carbamidomethyl was used as fixed modification, Gln- > pyro-Glu (N-term Q) was chosen as variable modification, and peptide tolerance was set at ±0.3 Da with a MH^+ mass values. The MOWSE score higher than 64 were considered to be credible identification of different proteins ($P < 0.05$).

Bioinformatics analysis of identified proteins

We used Web Gene Ontology Annotation Plot (WEGO) to classify all the identified differential proteins in terms of molecular function, cellular component and biological process (Ye et al., 2006). The Gene Ontology (GO) IDs of these identified differential proteins were obtained by InterProscan searching (http://www.ebi.ac.uk/Tools/InterProScan) using the amino acid sequences and output as txt format. The annotation files of up-regulated and down-regulated proteins were respectively integrated, named

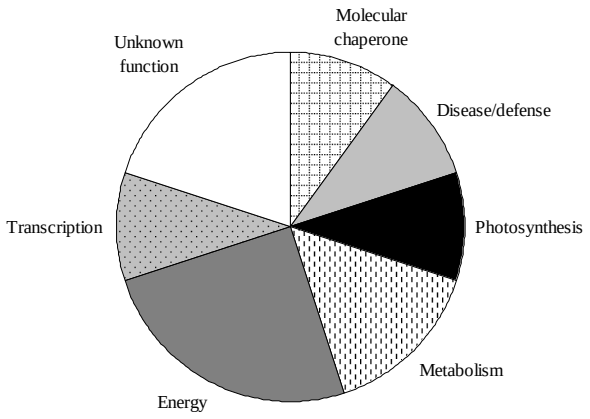

Fig 2. Functional categories of the identified proteins.

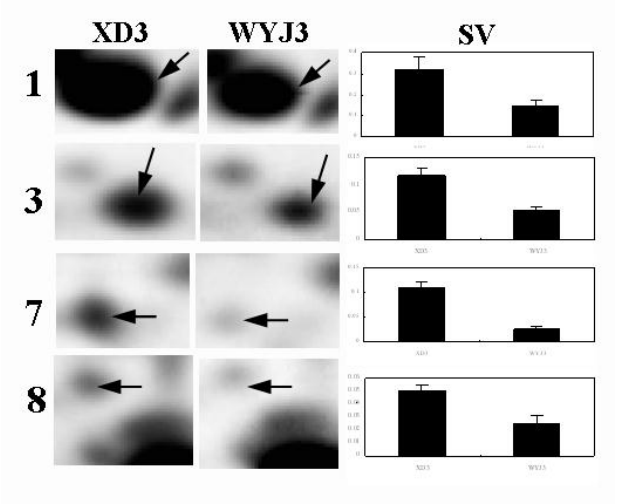

Fig 3. Enlarged view of distribution of stress or defense-related proteins. Changed proteins were indicated by black arrows, spot numbers were shown on the first column, and the quantitative changes of proteins were shown in the last column (SV: spot relative volume). Values are average of three replicates.

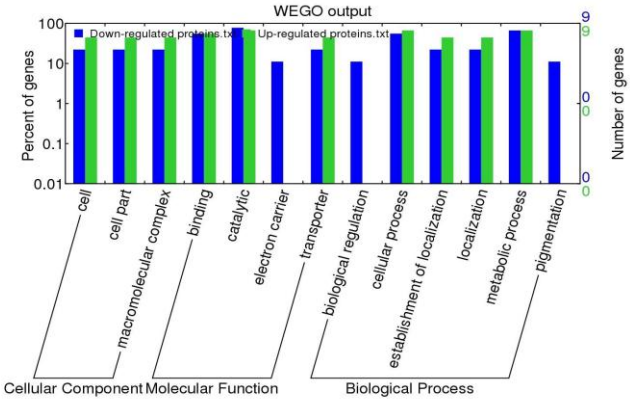

Fig 4. Categorization of the identified differentially expressed proteins of rice. These proteins were divided into 3 main categories and 13 subcategories.

and uploaded as InterproScan.txt into WEGO (http://wego.genomics.org.cn). Finally, the analysis result was exported as a histogram file (jepg format) after online operation.

Conclusions

The 2-DE method is efficient for proteomic analysis, and in present study more than 798 rice proteins could be detected in a single piece of gel. In all, 27 proteins were of significant differences in Xudao 3 and Wuyujing 3. 15 of them were up-regulated and 12 were down-regulated in Wuyujing 3, respectively, and 20 of them could be identified. Interestingly, four different proteins (spot 1, 3, 7, and 8) that have been shown to be implicated in stress and/or defense responses were also identified. They were significantly down-regulated in RSV-susceptible rice cultivars, and up-regulated in RSV-resistant rice cultivars, indicating they may be related to RSV-resistance. Our work not only provides candidate proteins and genes for subsequent studies but also suggests proteomic approach may be useful to identify novel proteins or genes in rice studies.

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