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Review

Proteomics of ionic stresses in rice: An overview

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Abstract Ions deficiency or excess remains one of the critical ground level environmental problems, affecting crop productivity. In this overview, we will discuss an increased application of proteomics technology in addressing this issue using rice (*Oryza sativa* L.) as a model crop plant. Proteomics analyses have revealed that rice proteome undergoes changes in the proteins composition and expression in response to several ionic stresses, including mineral nutrients (aluminum, nitrogen, and phosphorous) and heavy metals (arsenic, cadmium, and copper). Developed inventory of responsive proteins and their correlation with changes in physiological symptoms and parameters are a major step forward in: (i) better understanding the underlying mechanisms of ionic stresses-triggered responses in rice; (ii) comparative proteomics studies; and (iii) designing a novel strategy to improve crop plants.

Keywords Ionic stress, rice, proteomics

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Introduction

Rice (*Oryza sativa* L.) is a major edible crop contributing directly to growth and development of the human civilization in Asia by providing a source of nourishment in an easily utilizable form, namely the seed. However, its growth and grain (or seed) yield are dramatically affected by adverse environmental stresses (Agrawal et al. 2006, 2009; Agrawal and Rakwal 2006, 2008b, 2011). Heavy metals and excessive use of fertilizers are one of the growing environmental problems. Heavy metals are alone responsible for soil pollution of about 235 million hectares (Giordani et al. 2005). To study the effects of such pollutants is a major area of research in plant biology.

Proteomics technology has increasingly been utilized to understand the impact of environmental stresses on changes in the rice proteome, resulting in development of an inventory of responsive proteins (see a series of reviews, Agrawal et al. 2006, 2009; Agrawal and Rakwal 2003, 2006, 2008b, 2011). Such inventory has helped in constructing a working model and biology-driven hypothesis to overcome the environmental problems, including the ionic stresses. Ionic stress can be considered as an environmental problem that is by and large man-made. Therefore, it is ironic that we are now working hard to understand the effects of these stresses. In this regard, omics technologies including proteomics play a major role. Identified proteins are being used as potential biomarkers in dissecting the signaling and metabolic pathways responsive to ionic stresses and in crop breeding programs (see, Agrawal and Rakwal 2008a).
To date, there are nine proteomics-level studies, dealing with ionic stresses-triggered responses in rice. Those studies include aluminum (Al; Yang et al. 2007), nitrogen (N; Kim et al. 2009; Kim et al. unpublished results), phosphorous (P; Torabi et al. 2009), arsenic (As; Ahsan et al. 2008), cadmium (Cd; Aina et al. 2007; Lee et al.

2010), copper (Cu; Ahsan et al. 2007; Zhang et al. 2009), and multiple heavy metals (Hajduch et al. 2001). In this review, we will summarize these proteomics studies and discuss their impact on enhanced knowledge on ionic stresses-responsive proteins and regulatory mechanisms.

Ionic stresses in rice

Mineral nutrients

Mineral nutrients are crucial for normal plant growth and development, since they play important roles as cofactors in many enzymes with special functions (transcription factors, components of chloroplast and mitochondrial electron transport chain, and many more). Effects of some mineral nutrients (Al, N, and P) have been the subject of proteomics analyses (Fig. 1).

Aluminum (Al) excess

Toxicity of Al has been well documented in plants (Delhaize and Ryan 1995; Horst et al. 1999; Kollmeier et al. 2000; Marienfeld et al. 2000). It is generally known that toxic forms of Al are solubilized and accumulated into the soil solution at below pH 5.0, resulting in reduced shoot growth and crop yield (Kochian et al. 2005). Rice is one of the Al-tolerant crops. The first proteomics study investigated the effect of different concentrations of Al in roots (Yang et al. 2007) of the Al-resistant rice cultivar Xiangnuo 1 (XN1) (Xu et al. 2004). A total of 17 Al-responsive proteins were identified, where 12 and 5 proteins were up-regulated and down-regulated, respectively. Most of these proteins were functionally associated with signaling transduction, antioxidant, and detoxification. Several enzymes involved in reactive oxygen species (ROS) detoxification were up- regulated that included copper/zinc superoxide dismutase (Cu/Zn-SOD), glutathione

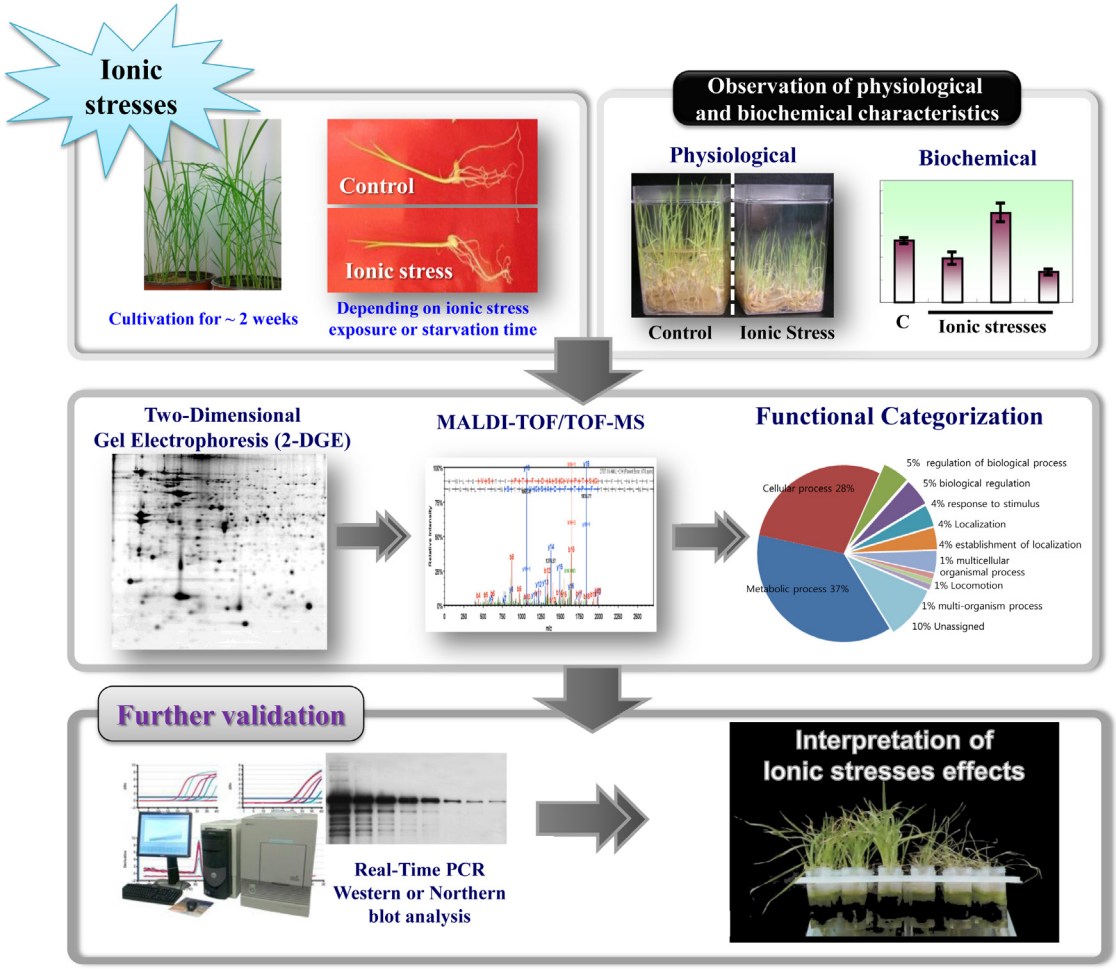

Fig. 1 Investigation of molecular responses in rice to ionic stresses. Usually two-week-old rice seedlings were used as an experimental system in combination with proteomics technology [such two-dimensional gel electrophoresis (2-DGE) with MALDI-TOF/TOF-MS or LC-MS/MS] to investigate changes in proteome to ionic stresses. Morphological changes in leaves and roots were observed due to ionic stresses

S-transferase (GST), and S- adenosylmethionine. Other Al up-regulated proteins were cysteine synthase (CS), 1-aminocyclopropane-1-carboxylate oxidase, G-protein β -subunit-like protein, abscisic acid- and stress-induced protein (ASR1), and putative Avr9/Cf-9 rapidly elicited protein. The CS protein could be of special interest as it might be involved in ion chelating during rice adaptation to Al.

To note, a few Al-responsive genes have been identified in rice (Yu et al. 1998; Mao et al. 2004) but it remains to be seen whether these data are functionally correlated as the modulation of mRNAs are not always consistent with the changes of protein and functions of the corresponding proteins (Griffin et al. 2002; Yan et al. 2006). Further work will be required to correlate the gene expression with protein abundance and functionality.

Nitrogen (N) deficiency

Nitrogen is essential for optimal plant growth and development (Marschner 1995). However, use of excessive N causes environmental contamination by denitrification, volatilization, soil erosion, microbial consumption, and leaching. To overcome these problems, there is a need to improve N utilization efficiency. Recently, considerable efforts have been made to validate several genes involved in N transport and metabolism (Hirel et al. 2007). Nevertheless, little is known about the molecular mechanisms regulating the adaptability of plants to N starvation. A first preliminary study using gel-based proteomics approach identified 41 differentially expressed low-N responsive proteins from a representative Indica cultivar BG90-2 leaf tissue using MALDI-TOF-MS and nESI-LC-MS/MS (Kim et al. 2009). These proteins were categorized mainly into energy metabolism (ATP synthesis, carbon fixation, TCA cycle, glycolysis and gluconeogenesis, nitrogen and sulfur metabolism), photosynthesis, oxidative stress, and as minor categories into amino acid transport and metabolism, defense/stress, iron homeostatis, posttranslational modifications, protein turnover & chaperones, and translation & ribosomal structure & biogenesis. To note, this study used hydroponically cultured three-week-old rice seedlings. Another proteomics-level study (Kim et al. unpublished results) studied the effects of N starvation in rice cultivar (Jinheung). Nitrogen starvation marginally increased root growth but notably decreased shoot biomass. Uptake of N was reduced greater than 50% in root and shoot. Twenty-five spots of differentially expressed proteins were analyzed by MALDI-TOF-MS and ESI-Q-TOF-MS. Identified proteins were mainly involved in protein synthesis & fate, carbohydrate metabolism, and defense. Some of these proteins were three luminal-binding proteins, 30S ribosomal protein, carboxyarabinitol-1, 5-bisphosphate, glyceraldehydes-3-phosphate dehydrogenase (GAPDH), NADP dependent malic enzyme, aconitate hydratase, GST, and two peroxidases.

Phosphorus (P) deficiency

Phosphorus is important for many biochemical and cellular processes including energy metabolism, photosynthesis, respiration, and biosynthesis of nucleic acids and membrane (Raghothama 1999; Vance et al. 2003). Effects of P starvation have been studied in roots of Nipponbare in comparison to its near isogenic line NIL6-4. The NIL6-4 carries a major QTL (Pup1) on chromosome 12 (Torabi et al. 2009). Thirty-two proteins showed dramatic changes in these two genotypes. Among them, 17 proteins differed in responses in two genotypes under low P concentration. Twenty-six proteins were identified by MALDI-TOF/TOF-MS and were found to be involved in P deficiency adaptation pathways, including reactive oxygen scavenging, citric acid cycle, signal transduction, and stress/defense responses. Of them, up-regulated stress- related enzymes included chloroplastic peroxiredoxin-2C, SOD, putative 1, 4-benzoquinonereductase, GST, ASR1, and chitinases, and were predominantly expressed except for salt-induced proteins (SalTs) in NIL6-4 line compared to Nipponbare. Similar response proteins in the two genotypes were pathogen-related (PR) proteins, such as the up-regulated chitinases and the down-regulated putative receptor-like protein kinase (RLK). These P-responsive proteins showed weak correlation with their corresponding mRNA levels; mRNA levels usually peaked before protein accumulation.

Heavy metals

Heavy metals are known to have inhibitory effects on many cellular processes in plant cells. Proteomics studies so far have dealt with effects of heavy metals As, Cd, and Cu in rice leaves and roots (Ahsan et al. 2007, 2008; Aina et al. 2007; Lee et al. 2010) and comparison of Cd, cobalt (Co), Cu, lithium (Li), mercury (Hg), strontium (Sr), and zinc (Zn) on rice leaves (Hajduch et al. 2001) (Fig. 2).

Arsenic (As)

Arsenic is well known as one of the toxic metalloids for both plants and animals. It is naturally occurring and present as a highly dissolved element in ground and surface waters by geochemical weathering of rocks, mi-

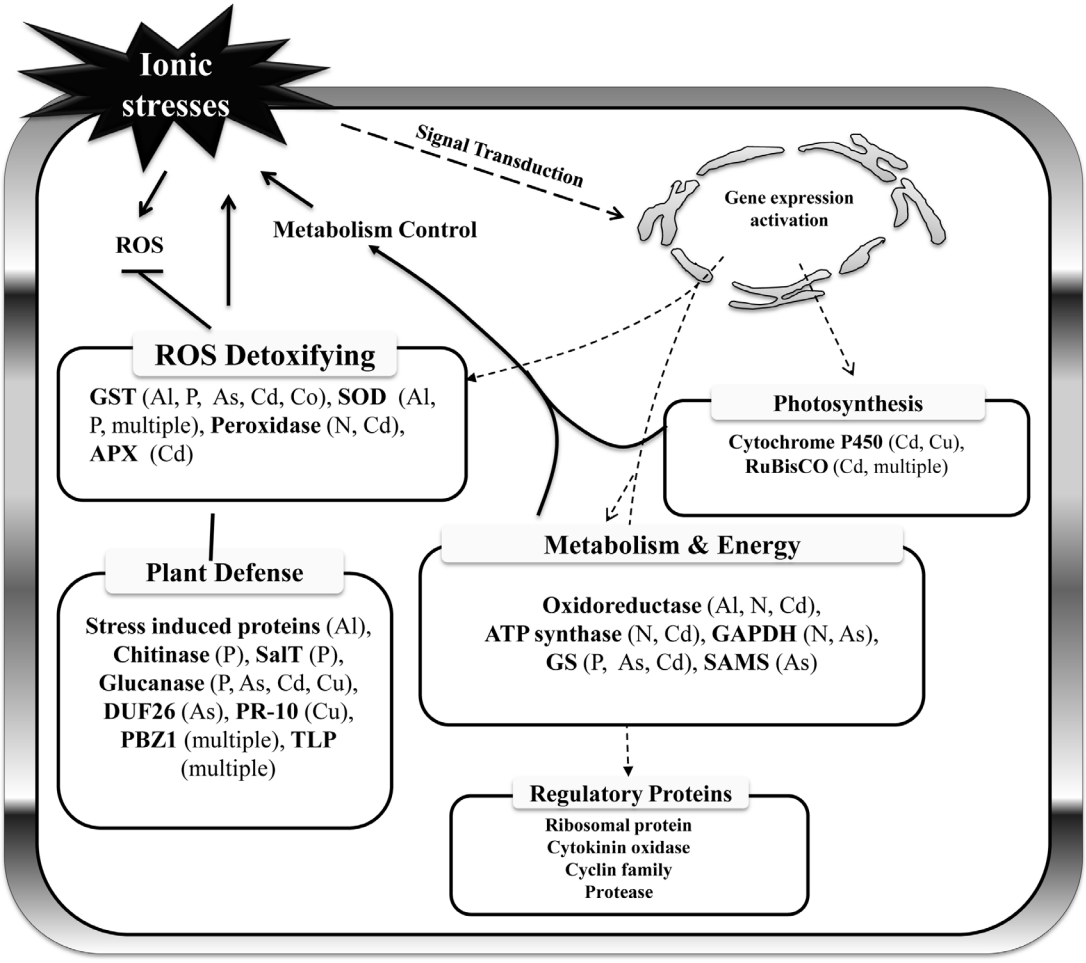

Fig. 2 An emerging model illustrating ionic stresses responsiveness in rice. Identified proteins of various biological functions were placed together to depict the ionic stresses triggered responses in rice. Abbreviations: APX, ascrobate peroxidase; DUF26, unknown domain family 26; GS, glutamine synthetase; GST, glutathione S-transferase; PBZ1, probenazole-inducible protein; PR-10, pathogen-related protein 10; ROS, reactive oxygen species; SAMS, S-adenosylmethionine synthetase; SalT, salt stress-induced protein; SOD, superoxide dismutase; TLP, thaumatin-like protein

crobial, and human activities (Meharg 2004). The presence or over-accumulation of As has become a global concern owing to the contamination of water, particularly in South-East Asia. However, little is known about As stress-elicited changes in plants at the proteome level. Recently, it was reported that rise in arsenic concentrations caused increased As accumulation, lipid peroxidation, GSH content, and hydrogen peroxide (H_2O_2) content in two-week-old rice seedlings (Ahsan et al. 2008). When two-week-old rice seedlings were subjected to As treatment for 4 days, there were a remarkably reduction in shoot and root growth. The As also had a profound effect on the root proteome, detecting 37 protein spots with more than 1.5-fold differences in expression values. Of the 23 spots identified by MALDI-TOF-MS, 17 and 6 were up- and down-regulated, respectively, by As treatment. Expression levels of stress and detoxification proteins, such as S-adenosylmethionine synthetase (SAMS), GSTs, CS, GST-tau, tyrosine-specific protein phosphatase proteins (TSPP), endo-1,3-b-D-glucosidase, DUF26-like protein, and SalT, were markedly increased. Of the down-regulated proteins were protein disulfide isomerase (PDI), nascent poly-peptide-associated complex (NAC), glutamine synthetase (GS), and GAPDH.

Cadmium (Cd)

Cadmium is one of the toxic heavy metal pollutants, and large amounts of Cd are released into the environment by human activities (Nriagu and Pacyna 1988). The Cd is easily imbibed by plants and can be accumulated throughout the food chain (Dudka and Miller 1999). To date, two independent proteomics studies were reported

on the Cd effect in rice root (Aina et al. 2007; Lee et al. 2010). Analogs to As and high concentrations of Cd also cause up-regulation of enzymes cooperating with GSH in ROS scavenging (GST). According to Lee and co-workers, most of proteins increased by 100 μM Cd in rice roots belonged to oxidative stress [three OsGSTUs, GSH reductase (GR), peroxidase, APX1, putative ferredoxin:NADP(H) oxidoreductase], PR proteins (PR-2, PR-5, PR-10), carbohydrate metabolism proteins, protein synthesis (chloroplast translational elongation factor Tu, elongation factor P), protein folding (putative chaperonin 60 beta), energy metabolism (ATP synthase F0 subunit 1, putative vacuolar proton-ATPase), and carbohydrate metabolism (bisphosphoglycerate-independent phosphoglyceratemutase, GAPDH, alpha-1,4-glucan-protein synthase) were up-regulated by 100 μM Cd treatment (Lee et al. 2010). The exposure to 10 μM Cd induced the expression of metabolic enzymes (alanine aminotransferase, hexokinase), transporters (ABC transporter-like protein, phosphate transporter, Nramp1), ubiquitin/proteasome pathway (26S proteasome, ubiquitin), and lignin biosynthesis (cynnamyl alcohol dehydrogenase) (Aina et al. 2007). In contrast, Cd treatments revealed repressive effects on the expression of enolase, chaperonin, cytochrome P450, peroxidase, and cyclin family (Aina et al. 2007; Lee et al. 2010).

Copper (Cu)

Copper is an essential micronutrient for plants, but excessive concentration of Cu can be toxic and inhibits the normal growth and development of plants (Caspi et al. 1999; Xiong and Wang 2005). Recently, proteomics analyses of copper effects in rice were reported by Ahsan et al. (2007) and Zhang et al. (2009). Ahsan et

Table 1 A list of rice proteomes in response to ionic stresses

Plant materials	Stress treatment	Morphology	DES[a] (ID[b])	Regulation trend	MFG[c]	Further validation	Ref.
Rice cv. Xiangnuo1 (4-leaf-stage seedling root)	0.1, 0.25 mM Al (pH 4.3, 12 and 36 h) and 2 mM Al (pH 4.3, 3 d)	10-20% reduction of root length	17 (17)	12(Up), 5 (Down)	Sulfur metabolism	Cysteine synthase activity and Western blot	Yang et al. (2007)
Rice cv. Jinheung (7-day-old seedling leaf)	Nitrogen deficiency (pH 5.8, 21 d)	~38% reduction of shoot length	25 (25)	19 (Up), 6 (Down)	Carbohydrate metabolism		Unpublished
Rice cv. Nipponbare and NIL6-4 (Root)	1 μM phosphorous (pH 5.0)	Reduction of root weight and tiller number	32 (26)	8 (Up), 18 (Down)	ROS metabolism	Real-Time PCR	Torabi et al. (2009)
Rice cv. Dongjin (2-week-old seedling root)	50, 100 μMAs (pH 5.5, 4 d)	Reduction of shoot and root growth	37 (23)	17 (Up), 6 (Down)	Stress and detoxifying-related proteins	Glutathione contents and enzyme activity	Ahsan et al. (2008)
Rice cv. Dongjin (Leaf and root)	100 μMCd (pH 5.8, 24 h)	Reduction of GSH contents in leaf and root	37 (36)	32 (Up), 4 (Down)	Antioxidant and carbohydrate metabolism	Northern blot	Lee et al. (2010)
Rice cv. Baldo (Seedling root)	10, 100 μM Cd (pH 5.8, 14 d)	Inhibition of plant growth	30 (21)	15 (Up), 6 (Down)	Regulatory and metabolic proteins	Gluthatione and phytochelatin analysis	Aina et al. (2007)
Rice cv. Hwayeong (Germinating seed)	0.2, 0.5, 1.0, 1.5, 2 mM Cu (4 d)	Reduction of seed germination rate	25 (25)	18 (Up), 7 (Down)	Detoxifying and stress-related proteins	Biomass and water contents	Ahsan et al. (2007)
Rice cv. Wuyunjing (Germinating seed)	200 μMCu (4~8 d)	Reduction of radicle length	16 (16)	13 (Up), 3 (Down)	Stress-related proteins	Protein-bound thiols assay	Zhang et al. (2009)
Rice cv. Nipponbare (Mature leaf)	250 μM Cu, Cd, Hg, Co, Li, Zn, and Sr (72 h)	Symptoms on leaf segments	33 (22)		Photosynthesis and pathogen-related proteins		Hajduch et al. (2001)

a: Differentially expressed protein spots; b: Identified proteins; c: Major functional groups

al. (2007) evaluated effects of elevated Cu concentrations on Cu-accumulating germinating rice seeds. Accumulations of Cu and thiobarbituric acid reactive substance (TBARS) content in seeds were increased significantly with increasing Cu concentrations. The 2-DGE analysis identified 25 differentially-expressed protein spots. Among them, 18 and 7 spots were up-regulated and down-regulated, respectively. Some antioxidant/stress-related proteins (glyoxalase I, peroxiredoxin, GST, dehydroquinatedehydratase, and aldose reductase) and regulatory proteins (DnaK-type molecular chaperone, UlpI protease, and RLK) were clearly up-regulated. The down-regulated metabolic proteins were alpha-amylase or enolase. Zhang et al. (2009) also reported Cu-responsive proteins in germinating embryos in rice cv. Wuyunjing. In that study, 16 proteins were identified using MALDI-TOF-MS. Thirteen of the proteins were up-regulated, including metallothionein-like protein, membrane-associated protein-like protein, putative wall-associated protein kinase, PR proteins, and the putative small GTP-binding protein Rab2. Three down-regulated proteins were a putative small cytochrome P450 (CYP90D2), a putative thioredoxin, and a putative GTPase.

Multiple heavy metals

To systemically analyze the metal effects on the rice leaves, Hajduch et al. (2001) reported changes in protein patterns after treatment with variety of metals, such as Co, Cu, Li, Hg, Sr, and Zn (Hajduch et al. 2001). These heavy metals led to formation of necrotic spots on leaves. Of 33 highly reproducible differential protein spots, 18 were identified by N-terminal or internal amino acid sequencing. A major photosynthetic protein ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) was heavily degraded in response to heavy metal (Hajduch et al. 2001). In contrast, expressions of ROS scavenging enzymes (Cu/Zn-SOD) and PR proteins (OsPR5 and OsPR10) were significantly increased.

Common aspects of plant response to ionic stresses at proteome level

Under ionic stresses, plant growth and development is inhibited, and is accompanied by oxidative damage and a down-regulation of the photosynthetic processes (Fig. 2). To overcome ionic stresses, plants induce biosynthesis of secondary stress-protective compounds (Fig. 2). Adaptation to stress in plants reveals enhanced requirements on detoxifying mechanism and energy metabolism (Fig. 2). Therefore, plants usually modulate antioxidant/stress-related proteins and carbohydrate proteins for enhancing tolerance to a given stress factor. Enhanced ROS formation induces enhanced expression of ROS scavenging enzymes, mainly enzymes participating in ascorbate-glutathione cycle or GST (Ahsan et al. 2008; Aina et al. 2007; Lee et al. 2010; Yang et al. 2007). Increased concentrations of heavy metals cause increased expression of chelating proteins, especially phytochelatins (PCs), derivatives of GSH (Aina et al. 2007; Lee et al. 2010; Zang et al. 2009). Proteomics-based results indicate that tolerant plants can induce several protective mechanisms more efficiently than sensitive ones, and thus, they are able to maintain sufficient rates of oxidative stress defense enzymes (Torabi et al. 2009). Maintenance of sufficient rates of processes associated with energy metabolism is important for an efficient stress acclimation, since plant stress acclimation is an active process associated with *de novo* biosynthesis of several stress-protective compounds. Hence, it is characterized by enhanced energy requirements (Aina et al. 2007; Lee et al. 2010; Yang et al. 2007). Studies of changes in proteome composition under stress are highly important, since they can help us to uncover key proteins involved in mechanisms underlying plant acclimation to stress.

Concluding remarks

Proteomics of ionic stresses in rice has undoubtedly increased our knowledge on proteins responsive to different-types of ionic stresses. Identified proteins have provided a better picture on underlying mechanisms of ionic stresses in rice (Figs. 1, 2). Yet, ionic stresses-response rice proteome need comprehensive investigation using parallel proteomics approaches to generate its near complete proteome. Near complete list of responsive proteins are required to lay a strong foundation for further functional analysis, including protein modification, protein networks, and functional dissection of proteins.

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