INTRODUCTION

Rice is the one of the key model plants for research and also the major food crop in developing countries. Dramatic increases in rice production have occurred in the past few decades through large scale hybrid rice cultivation using cytoplasmic male sterile (CMS) lines with abortive pollen caused by dysfunctional mitochondria (Eckardt, 2006; Wang et al., 2006). This tremendous advance highlights the significance of understanding rice mitochondrial function. The role and nature of rice mitochondria also takes on special significance due to its early growth in hypoxic or even anoxic environments (Perata and Voosenek, 2007) as well as its need for rapid mitochondrial biogenesis and function during re-oxygenation (Millar et al., 2004; Howell et al., 2007). Mitochondria contain many hundreds of different proteins that initiate or co-ordinate the biochemical processes essential for its function. It is estimated that while only ∼300 proteins are components of the respiratory apparatus, up to 2000 proteins are housed in plant mitochondria with the majority encoded in the nucleus and transported into mitochondria as cytosolic precursor proteins by the mitochondrial protein import machinery (Millar et al., 2005; Cui et al., 2011). Because software-based subcellular targeting prediction offers low fidelity in actual subcellular localization (Hazlewood et al., 2004, 2005), direct experimental analysis of mitochondrial proteomes, including that of rice, is required to obtain precise information on which proteins are mitochondrially located. More broad advances in rice proteomics have been well summarized recently (Agrawal and Rakwal, 2011). In this review, recent research on rice mitochondrial purification, contaminant removal, and rice mitochondrial proteomic analysis are discussed. The rice mitochondrial protein composition, functional classifications, and features of mitochondrial protein presences are summarized. We also discuss the effects of the environment, in particular anoxia and light, on rice mitochondrial proteome composition and how the proteome differs in CMS lines. Finally, we propose future directions for research on the rice mitochondrial proteome.

PURIFICATION AND PROTEOMIC ANALYSIS OF RICE MITOCHONDRIA

Removal of contaminants, like chloroplasts, from purified rice mitochondria is critical for downstream protein separation and identification of mitochondrial proteins. Classically, differential and gradient centrifugation methods based on size and density have been applied to plant mitochondrial proteomic analysis (Kruft et al., 2001; Millar et al., 2001; Bardel et al., 2002). Using these approaches, mitochondria have been purified on Percoll density gradients from dark-grown rice seedlings (Hazlewood et al., 2005) and from green rice seedlings (Kristensen et al., 2004).
The purified mitochondria from dark-grown seedlings were then separated using 2-D IEF/SDS-PAGE, blue native (BN)-PAGE and 122 proteins were identified using LC-MS/MS (Heazlewood et al., 2003). In another similar study that used a sucrose gradient for mitochondrial purification, a set of 112 non-redundant rice mitochondrial proteins were identified after 2-D IEF/SDS-PAGE separation (Komatsu, 2005). Comparison of these two studies revealed less than 20% overlap in the two datasets of highly abundant proteins, highlighting the importance of optimized methods for mitochondria purification prior to proteomic analysis.

Free-flow electrophoresis in zone electrophoresis mode (ZE-FFE) can be used to separate organelles based on differential surface charge and this has allowed the comprehensive analysis of Arabidopsis organelar proteomes including the exclusion of contaminating proteins through quantitative analysis (Eubel et al., 2007, 2008). The combination of traditional differential and gradient centrifugation with this new FFE separation technique has allowed isolation of highly purified rice mitochondria for proteomic analysis (Huang et al., 2009a). Quantitative analysis using differential in gel electrophoresis (DIGE) and spectral counting have allowed the identification of contaminant proteins removed by FFE purification (Huang et al., 2009a). The purity of isolated mitochondria was >95% based on calculating the number of peptides from contaminant proteins compared to peptides from mitochondrial proteins in these preparations (Huang et al., 2009a).

In total, 322 proteins from FFE purified rice mitochondria were identified through the direct analysis of trypsin-digested peptides by LC-MS/MS and gel-based analysis (Huang et al., 2009a). The annotations of rice mitochondrial protein spots on 2-D IEF/SDS/PAGE gel are available online using the gel-map tool (Klodmann et al., 2011; Senkler and Braun, 2012). Seventy-eight proteins identified previously as components of the rice mitochondrial proteome (Heazlewood et al., 2003) were also in this study. Half of the unconfirmed proteins from Heazlewood et al. (2003) were proteins now predicted to be retrotransposon sequences with unknown function.

**THE PROTEIN COMPOSITION OF RICE MITOCHONDRIA**

A refined dataset of 322 proteins allowed us to assess the functional distribution of the rice mitochondrial proteome as shown in Figure 1. There are 99 proteins identified as either components of the five oxidative phosphorylation/respiratory complexes or TCA cycle enzymes, representing 31% of the total set (Figure 1). The genes encoding electron transport chain (ETC) proteins are highly expressed across all tissues, which is consistent with the fundamental role of mitochondria in energy production throughout the plant. Interestingly, a series of genes encoding TCA cycle components are highly expressed in anthers, suggesting a high energy requirement for metabolism in this tissue (Huang et al., 2009a). There were 64 proteins identified (20% of total set) that are
thought to be involved in central carbon and nitrogen metabolism (Figure 1), such as the interconversion of amino acids, photorespiratory glycerol oxidation, synthesis of lipids, vitamins, as well as export of organic acids. Within this group, the identification of a 4-methyl-5-thiazole monophosphate biosynthesis protein (Os01g11880) provided new insight into the involvement of rice mitochondria in the process of thiamine biosynthesis. Furthermore, the highly selective expression of genes for components of photorespiratory glycerol oxidation in leaf tissues is consistent with the role of mitochondria in photorespiration during photosynthesis in green tissues (Huang et al., 2009a). Proteins involved in supporting machinery such as those for DNA replication, transcription and translation, protein import and fate, ETC assembly as well as carriers and transporters accounted for 21% of the total number of proteins identified. Thirty-three proteins were listed to be involved in DNA replication, transcription, and translation, and 19 proteins were assigned the protein import and fate category (Figure 1). Genes encoding mitochondrial enzymes involved in DNA replication, transcription, and translation, as well as protein import and fate are highly expressed in early germinated rice seeds as well as in suspension culture cells, consistent with their role in mitochondrial biogenesis (Huang et al., 2009a). Fifteen heat shock proteins and 9 putative stress response proteins were also identified (Figure 1). A total of 55 proteins (17%) were identified for which no known function has been reported (Figure 1).

From the 313 nuclear-encoded rice mitochondrial proteins identified, ~63% were predicted to be located in mitochondria by four different subcellular localization prediction software packages (Huang et al., 2009a). The low fidelity of the prediction software is due in part to the use of a limited number of targeting signals in training sets for these software packages (Heazlewood et al., 2004), which again highlights the importance of building experimental evidence for the mitochondrial location of proteins. The number of identified proteins involved in the ETC and TCA cycle in monocotyledon rice mitochondria is similar to number of identified proteins involved in the ETC and TCA cycle in monocotyledon Arabidopsis mitochondria (Huang et al., 2004) and the corresponding proteins are also largely conserved (Huang et al., 2011). Proteins involved in supporting machinery and stress response were also conserved between the rice and Arabidopsis datasets (Huang et al., 2011). The conservation of the proteomes between these diverse species highlights the fundamental role of mitochondria in energy production and metabolism in plants.

**THE RICE MITOCHONDRIAL PROTEIN PRESEQUENCE AND ITS CLEAVAGE**

N-terminal presequences carry the targeting signals required to import nuclear-encoded mitochondrial proteins and these are cleaved off following the import process to generate mature proteins (Zhang and Glaser, 2002). Analysis of the peptides derived from the digestion of mature rice mitochondrial proteins allowed us to experimentally identify cleavage sites and thus determine 52 rice mitochondrial presequences (Huang et al., 2009b). The average length of these presequences is 45 amino acids. The average pI of the first 10 amino acids was 11.8 with a hydrophobicity index of -1.4. Nearly 90% of the presequences were predicted to form α-helices in this region (Huang et al., 2009b). These features are very similar to those observed for Arabidopsis mitochondrial proteins (Huang et al., 2009b).

Amongst the rice mitochondrial presequences three groups of cleavage sites were found: -2 Arg (class I), -3 Arg (class II); and one without any conserved Arg (class III; Figure 2). The majority of presequences were -3 Arg (38%) with a smaller contingent of -2 Arg (13%), and a surprisingly large percentage without any conserved arginine (29%; Figure 2). In the dominating -3 Arg group, the occurrence of Tyr/Phe/Leu at the -1 position was evenly distributed (Figure 2), which differs from the similar Arabidopsis -3 Arg group which predominantly features Phe at the -1 position (Huang et al., 2009b). In yeast, an intermediate cleaving peptidase (Icp55, P40051) removes one residue from the presequence after cleavage by the mitochondrial processing peptidase (MPP) when it contains an Arg residue at the -3 position (Viglile et al., 2009). It is likely that in the mitochondria of rice and Arabidopsis, the observed -3 Arg proteins are a consequence of an Icp55-like cleavage, after MPP cutting by an uncharacterized peptidase (Figure 2). Yeast Icp55 (P40051) does have a rice ortholog (Os12g37640; E = 2 × e^-91). We have not found Os12g37640 in the rice mitochondrial protein data set (Huang et al., 2009a), but it is predicted to be located in mitochondria by Target P and Mitoprot II. Future functional analysis of Icp55-like peptidase in plant mitochondria is needed to understand its role in stabilizing mitochondrial proteins following MPP cleavage.

**CHANGES IN THE RICE MITOCHONDRIA PROTEOME DURING ENVIRONMENTAL STRESS AND PLANT DEVELOPMENT**

Most rice proteomic analyses in response to environmental stresses have been conducted at the whole tissue level in leaves or leaf sheaths. Mitochondrial proteins contribute only ~2–5% of total cellular protein and this makes them difficult to quantify in whole tissue protein extracts. For example, there no mitochondrial proteins with significant changes in abundance were detected in rice leaves or sheaths under drought (Salekdeh et al., 2002; Ali et al., 2003). A total of 15 heat shock proteins and 9 putative stress response proteins were also identified (Figure 1). A total of 55 proteins (17%) were identified for which no known function has been reported (Figure 1). From the 313 nuclear-encoded rice mitochondrial proteins identified, ~63% were predicted to be located in mitochondria by four different subcellular localization prediction software packages (Huang et al., 2009a). The low fidelity of the prediction software is due in part to the use of a limited number of targeting signals in training sets for these software packages (Heazlewood et al., 2004), which again highlights the importance of building experimental evidence for the mitochondrial location of proteins. The number of identified proteins involved in the ETC and TCA cycle in monocotyledon rice mitochondria is similar to number of identified proteins involved in the ETC and TCA cycle in monocotyledon Arabidopsis mitochondria (Huang et al., 2004) and the corresponding proteins are also largely conserved (Huang et al., 2011). Proteins involved in supporting machinery and stress response were also conserved between the rice and Arabidopsis datasets (Huang et al., 2011). The conservation of the proteomes between these diverse species highlights the fundamental role of mitochondria in energy production and metabolism in plants.

![Image](https://www.frontierin.org)
and salt (Kim et al., 2005; Chitteti and Peng, 2007). It is clear that proteins are oxidized in the matrix of mitochondria for protein oxidation analysis, it was found that a number of proteins are oxidized in the matrix in vivo and a group of proteins are particularly susceptible to mild oxidation in vitro (Kristensen et al., 2004).

The early growth habit of rice is often hypoxic or even anoxic (Perata and Vossek et al., 2007), meaning that the role and nature of rice mitochondria is especially interesting given their central role in respiration. An early study showed that anoxic rice shoots had the ability to synthesize the same range of mitochondrial proteins as aerobically grown shoots as long as ATP was supplied, which could be provided in vivo by glycolytic reactions even in the absence of oxygen (Cousie et al., 1992). Analysis of the soluble rice mitochondrial proteome using 2-D IEF/SDS-PAGE gel separation showed no significant difference between samples derived from aerobic and reoxygenated coleoptiles (Millar et al., 2004). However, BN-SDS-PAGE gels of mitochondrial membrane-associated complexes showed a very low abundance of assembled b(6) complex and cytochrome c oxidase in anoxic samples and a dramatic increase in the abundance of these complexes after 1 day of air adaptation (Miller et al., 2004). These results suggested that anoxic rice does have the capacity to develop its respiratory machinery, but with a discrete and reversible blockage of full mitochondrial biogenesis at Complex III (Millar et al., 2004). In a whole-cell proteomic analysis, malate dehydrogenase and two ATP synthase subunits were lower in abundance in 6-day-old anoxic coleoptiles compared to similar sized 4-day-old aerated coleoptiles (Shingaki-Wells et al., 2011). The lower abundance of enzymes involved in the TCA cycle or ETC with a fourfold increase in the photorespiration rate of low light-treated plants compared to those treated with high light (Huang et al., 2013).

Cytoplasmic male sterility is a fundamental part of hybrid rice production and relies on plant lines with pollenspecific defects in mitochondrial function (Eckardt, 2006; Wang et al., 2006). Most CMS-associated genes in rice are chimerics composed of a fragment of a normal mitochondrial gene, encoding small and low abundance mitochondrial membrane proteins, and a novel and disruptive sequence that influences the expression or the function of the gene product (Hansson and Bengtson, 2004; Kubo and Newton, 2008). Quantitative proteomic analysis of CMS-related changes in rice anthers has revealed eight proteins with abundances that are at least twofold lower or higher when comparing CMS (CMS) and YTB (isogenic fertile) lines (Sun et al., 2009). However, none of these were mitochondrially encoded proteins. Further quantitative analysis of the mitochondrial proteomes from 10-day-old rice seedlings has revealed a reduced abundance of specific proteins in mitochondrial complexes, particularly complex V, in the CMS line compared with the YTB line (Liu et al., 2012). Interestingly, a sex determination TASSELSEED-2-like protein (Os07g46920) was found 3.2-fold more abundant in the CMS line (Liu et al., 2012). Analysis of the potential links between the increase in the amount of this protein and jasmonic acid production and salt (Kim et al., 2005; Chitteti and Peng, 2007). It is clear that to obtain a more detailed picture of the mitochondrial proteome in response to different environmental stresses, purified mitochondria would be required. Using isolated rice mitochondria for protein oxidation analysis, it was found that a number of proteins are oxidized in the matrix in vivo and a group of proteins are particularly susceptible to mild oxidation in vitro (Kristensen et al., 2004).

The early growth habit of rice is often hypoxic or even anoxic (Perata and Vossek et al., 2007), meaning that the role and nature of rice mitochondria is especially interesting given their central role in respiration. An early study showed that anoxic rice shoots had the ability to synthesize the same range of mitochondrial proteins as aerobically grown shoots as long as ATP was supplied, which could be provided in vivo by glycolytic reactions even in the absence of oxygen (Cousie et al., 1992). Analysis of the soluble rice mitochondrial proteome using 2-D IEF/SDS-PAGE gel separation showed no significant difference between samples derived from aerobic and reoxygenated coleoptiles (Millar et al., 2004). However, BN-SDS-PAGE gels of mitochondrial membrane-associated complexes showed a very low abundance of assembled b(6) complex and cytochrome c oxidase in anoxic samples and a dramatic increase in the abundance of these complexes after 1 day of air adaptation (Miller et al., 2004). These results suggested that anoxic rice does have the capacity to develop its respiratory machinery, but with a discrete and reversible blockage of full mitochondrial biogenesis at Complex III (Millar et al., 2004). In a whole-cell proteomic analysis, malate dehydrogenase and two ATP synthase subunits were lower in abundance in 6-day-old anoxic coleoptiles compared to similar sized 4-day-old aerated coleoptiles (Shingaki-Wells et al., 2011). The lower abundance of enzymes involved in the TCA cycle or ETC with a fourfold increase in the photorespiration rate of low light-treated plants compared to those treated with high light (Huang et al., 2013).
metabolism has identified a lesion in the jasmonic acid synthesis pathway during the development of microspores in CMS plants (Liu et al., 2012).

**FUTURE DIRECTIONS**

The plant mitochondrial proteome is a changing entity over time, in different tissues/organs and in response to different environments, as revealed by discoveries made in mitochondrial proteome research of the dicotyledon model plant Arabidopsis (Sweetlove et al., 2002; Lee et al., 2008, 2011; Tan et al., 2012). The rice mitochondrial proteome is likely to share these dynamics based on the analysis of rice transcript data for genes encoding mitochondrial proteins (Ishiguro et al., 2004). Differential induction of mitochondrial machinery by light intensity correlates with changes in respiratory metabolism and photosynthesis in rice leaves. New Phytol. doi: 10.1111/j.1469-8137.2012.04014.x (in press).

Huang, S., Jewell, R. P., Shanqki-Wells, B. N., Li, L., and Miller, A. H. (2013). Differential induction of mitochondrial machinery by light intensity correlates with changes in respiratory metabolism and photosynthesis in rice leaves. New Phytol. doi: 10.1111/j.1469-8137.2012.04014.x (in press).

Huang, S., Miller, A. H., and Taylor, N. L. (2011). “The plant mitochondrial proteome composition and stress response: conservation and divergence between monocots and dicots.” In *Plant Mitochondria*. Advances in Plant Biology, Vol. I, ed. F. Kampa-Holmes (New York: Springer Science+Business Media), 207–259.

Huang, S., Taylor, N. L., Narsai, R., Eubel, H., Whelan, J., and Millar, A. H. (2010a). “Experimental analysis of the rice mitochondrial proteome, its biogenesis, and heterogeneity.” Plant Physiol. 154, 719–734.

Huang, S., Taylor, N. L., Whelan, J., and Millar, A. H. (2006). “Combining computational and experimental data for determination of the subcellular location of proteins in Arabidopsis.” Plant Physiol. 139, 598–609.

Huang, S., Taylor, N. L., Narsai, R., Eubel, H., Whelan, J., and Millar, A. H. (2006). “Experimental analysis of the Arabidopsis mitochondrial proteome highlights signaling and regulatory components, provides assessment of targeting prediction programs, and indicates plant-specific mitochondrial proteins.” Plant Cell 18, 615–629.

Hübner, K. M., Shew, H. J., and Lamping, I. A. (2005). “Using Ca2⁺ photophorase to increase the yield of rice: a rationale and feasibility.” *Crop. Caryologia* 58, 255–264.

Eubel, H., Meyert, E. H., Taylor, N. L., Buol, J. D., O’Toole, N., Huang, S., and Millar, A. H. (2004). “Novel proteins, putative membrane transporters, and an integrated metabolic network are revealed by quantitative proteomic analysis of Arabidopsis cell culture peroxisomes.” Plant Physiol. 139, 1809–1829.

Huang, S., Jowett, R. P., Shanqki-Wells, B. N., Li, L., and Miller, A. H. (2013). “Differential induction of mitochondrial machinery by light intensity correlates with changes in respiratory metabolism and photosynthesis in rice leaves.” New Phytol. doi: 10.1111/j.1469-8137.2012.04014.x (in press).

Huang, S., Jewell, R. P., Shanqki-Wells, B. N., Li, L., and Miller, A. H. (2013). “Differential induction of mitochondrial machinery by light intensity correlates with changes in respiratory metabolism and photosynthesis in rice leaves.” New Phytol. doi: 10.1111/j.1469-8137.2012.04014.x (in press).

Huang, S., Miller, A. H., and Taylor, N. L. (2011). “The plant mitochondrial proteome composition and stress response: conservation and divergence between monocots and dicots.” In *Plant Mitochondria*. Advances in Plant Biology, Vol. I, ed. F. Kampa-Holmes (New York: Springer Science+Business Media), 207–259.

Huang, S., Taylor, N. L., Narsai, R., Eubel, H., Whelan, J., and Millar, A. H. (2010a). “Experimental analysis of the rice mitochondrial proteome, its biogenesis, and heterogeneity.” Plant Physiol. 154, 719–734.

Huang, S., Taylor, N. L., Whelan, J., and Millar, A. H. (2006). “Combining computational and experimental data for determination of the subcellular location of proteins in Arabidopsis.” Plant Physiol. 139, 598–609.

**REFERENCES**

Appraw, K. C., and Balaban, R. (2011). “Rice proteomics: a more toward expanded proteome coverage to comparative and functional proteomics uncovers the mysteries of rice and plant biology.” Proteomics 11, 1635–1649.

Ali, G. M., and Komatsu, S. (2006). “Cytoplasmic metabolism in different tissues/organs and in response to different environments, as revealed by discoveries made in mitochondrial proteome research of the dicotyledon model plant Arabidopsis.” Sweetlove et al., 2002; Lee et al., 2008, 2011; Tan et al., 2012). The rice mitochondrial proteome is likely to share these dynamics based on the analysis of rice transcript data for genes encoding mitochondrial proteins (Ishiguro et al., 2004). Differential induction of mitochondrial machinery by light intensity correlates with changes in respiratory metabolism and photosynthesis in rice leaves. New Phytol. doi: 10.1111/j.1469-8137.2012.04014.x (in press).
Huang et al. Rice mitochondrial proteome and stress response

Lee, J., Bröcker, T. M., Lefèvre, M., Petson, S. R. M., and Oard, J. H. (2006). Proteomics and genetic approaches to identifying defence-related proteins in rice challenged with the fungal pathogen Rhizoctonia solani. Mol. Plant Pathol. 7, 405–416.

Liu, G., Tian, H., Huang, Y.-Q., Hu, J., Ji, Y.-X., Li, S.-Q., et al. (2012). Alterations of mitochondrial protein assembly and jasmonic acid biosynthetic pathway in Honglian (S13-type cytoplasmic male sterility rice). J. Plant Physiol. 169, 4093–4100.

Millar, A. H., Haoudi, J. L., Kreis, J. M., Braam, H. J., and Millar, A. J. (2005). The plant mitochondrial proteome. Trends Plant Sci. 10, 36–43.

Millar, A. H., Sweetlove, L. J., G趋, P., and Leaver, C. J. (2001). Analysis of the Arabidopsis mitochondrial proteome. Plant Physiol. 127, 1711–1727.

Millar, A. H., Trend, A. E., and Heazlewood, J. L. (2004). Changes in the mitochondrial proteome during the anaerobic to aerobic transition in rice focus around cytochrome-containing respiratory complexes. J. Biol. Chem. 279, 39471–39478.

Peraza, P., and Voesenek, L. A. C. J. (2007). Submergence tolerance in rice requires Sul1AB, an ethylene-response-factor-like gene. Trends Plant Sci. 12, 43–46.

Sakkad, H. G., Suppongong, J., Wada, L. J., Ohraymzade, B., and Bennett, J. (2002). Proteomic analysis of rice leaves during drought stress and recovery. Proteomics 2, 1155–1165.

Tekle, M., and Braun, H.-P. (2012). Functional annotation of 2D protein maps: the GelMap portal. Proteomics Sci. 3, 877–879 doi: 10.5890/pis.2012.08077.

Shingale-Wells, R. N., Huang, S., Taylor, N. L., Howell, K. A., Heazlewood, J. L., Taylor, N. L., and Millar, A. H. (2011). Differential molecular response of rice and wheat coleoptiles to anoxia following exposure to cold and chemical stresses. Plant Physiol. 156, 1705–1724.

Sun, Q., Hu, C., Hu, J., Li, S., and Zhu, Y. (2009). Quantitative proteomic analysis of CMS-related changes in Honglian CMS rice anther. Proteomics J 28, 341–348.

Sweetlove, L. J., Haoudi, J. L., Harold, V., Houbreipfl, R., Due, D. A., Leaver, C. J., et al. (2002). The impact of oxidative stress on Arabidopsis mitochondria. Plant J. 52, 391–404.

Tan, Y.-F., Millar, A. H., and Taylor, N. L. (2012). Components of mitochondrial oxidative phosphorylation vary in abundance following exposure to cold and chemical stresses. J. Proteome Res. 11, 3860–3879.

Taylor, N. L., Howell, K. A., Heazlewood, J. L., Tan, T. W. Y., Narasim, R., Huang, S., et al. (2010). Analysis of the rice mitochondrial carrier family reveals anoxic accumulation of a basic amino acid carrier involved in arginine metabolism during seed germination. Plant Physiol. 156, 691–704.

Turner, S. R., Hall, E., Inland, B., Ellis, N., and Rawsthorne, S. (1993). The organization and expression of the gene encoding the mitochondrial glycine decarboxylase complex and serine hydroxymethyltransferase in pea (Pisum sativum). Mol. Gen. Genet. 236, 402–408.

Viegha, F. N., Mørkholm, S., Zahedi, R. P., Becker, D., Leishold, C., Geraert, K., et al. (2005). Global analysis of the mitochondrial N-proteome identifies a processing peptide critical for protein stability. Cell 120, 428–439.

Walker, J. L., and Oliver, D. J. (1996). Light-induced increases in the glycine decarboxylase multienzyme complex from pea leaf mitochondria. Arch Biochem. Biophys. 246, 626–634.

Wang, W., Sun, Y., Li, X., Zhang, Q., Chen, L., Wu, H., et al. (2008). Cytoplasmic male sterility of rice with Boro II cytoplasm is caused by a cytosolic peptide and is restored by two related PPR motif genes via distinct modes of mRNA elongation. Plant Cell 19, 670–687.

Yan, S.-P., Zhang, Q.-Y., Tang, Z.-C., Su, W.-A., and Sun, W.-N. (2006). Comparative proteomic analysis provides new insights into chilling stress responses in rice. Mol. Cell. Proteomics 5, 484–496.

Zhang, X. P., and Glaser, E. (2002). Interaction of plant mitochondrial and chloroplast signal peptides with the Hip70 molecular chaperone. Trends Plant Sci. 7, 14–21.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 18 December 2012; accepted: 22 January 2013; published online: 07 February 2013.

Citation: Huang S, Shingaki-Wells RN, Taylor NL and Millar AH (2013) The rice mitochondrial proteome and its response during development and in the environment. Front. Plant Sci. 4:16. doi: 10.3389/fpls.2013.00016

This article was submitted to Frontiers in Plant Proteomics, a specialty of Frontiers in Plant Science.

Copyright © 2013 Huang, Shingaki-Wells, Taylor and Millar. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in other forums, provided the original authors and source are credited and subject to any copyright notices concerning any third-party graphics etc.