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Defining the plant peroxisomal proteome: from *Arabidopsis* to rice

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Peroxisomes are small subcellular organelles mediating a multitude of processes in plants. Proteomics studies over the last several years have yielded much needed information on the composition of plant peroxisomes. In this review, the status of peroxisome proteomics studies in *Arabidopsis* and other plant species and the cumulative advances made through these studies are summarized. A reference *Arabidopsis* peroxisome proteome is generated, and some unique aspects of *Arabidopsis* peroxisomes that were uncovered through proteomics studies and hint at unanticipated peroxisomal functions are also highlighted. Knowledge gained from *Arabidopsis* was utilized to compile a tentative list of peroxisome proteins for the model monocot plant, rice. Differences in the peroxisomal proteome between these two model plants were drawn, and novel facets in rice were expounded upon. Finally, we discuss about the current limitations of experimental proteomics in decoding the complete and dynamic makeup of peroxisomes, and complementary and integrated approaches that would be beneficial to defining the peroxisomal metabolic and regulatory roadmaps. The synteny of genomes in the grass family makes rice an ideal model to study peroxisomes in cereal crops, in which these organelles have received much less attention, with the ultimate goal to improve crop yield.

Keywords: peroxisome, proteomics, *Arabidopsis*, rice

INTRODUCTION

Eukaryotic cells compartmentalize specific biochemical reactions in membrane-bound subcellular organelles. Peroxisomes are small and dynamic single membrane-delimited organelles found in nearly all eukaryotic cells and perform a wide array of functions, which differ in different organisms and even vary depending on the tissue type and prevailing environmental conditions. Although peroxisomes in different organisms exhibit significant functional heterogeneities, two peroxisomal functions, i.e., β-oxidation of fatty acids and hydrogen peroxide (H_2O_2) catabolism, are universal. Strong defects in peroxisome biogenesis or core peroxisome metabolic functions lead to fatal disorders in humans and embryonic lethality in plants (Schrader and Fahimi, 2008; Kaur et al., 2009).

In the absence of a genome, the entire peroxisome protein complement is comprised of proteins that are nuclear encoded and translated on cytosolic ribosomes prior to import into the organelle. Further, peroxisomes are distinguished from other organelles by their ability to import fully folded proteins into the organelle matrix. The presence of conserved peroxisome targeting signals (PTSs) in the peroxisome matrix proteins facilitates their recognition by cytosolic receptors. These PTSs comprise of two types: the C-terminal tripeptide PTS1 (SKL and derivatives thereof), and the N-terminal nonapeptide PTS2 (RLX_5HL and derivatives) that is cleaved post-import in mammals and plants. Once bound by the cytosolic receptors, the PTS-containing proteins are transported to the peroxisome membrane and delivered into the matrix, aided by several peroxisome membrane-associated proteins that form the docking complex and the importomer (Rucktaschel et al., 2011).

Peroxisomes serve as essential "nodes" in a number of metabolic networks within the cell through physical and metabolic links with other cellular compartments such as mitochondria, chloroplasts, and oil bodies. Besides their roles in β-oxidation of fatty acids and degradation of H_2O_2, plant peroxisomes also mediate pathways such as photorespiration, jasmonic acid biosynthesis, indole 3-butyric acid (IBA) metabolism, glyoxylate cycle, purine degradation, and further contribute toward pathogen defense and essential developmental processes such as embryogenesis and photomorphogenesis (Hayashi and Nishimura, 2003; Baker et al., 2006; Reumann and Weber, 2006; Kaur et al., 2009; Palma et al., 2009). The major protein constituents of plant peroxisomes had been well characterized, yet the complete makeup of these organelles was far from being decoded. Understanding the metabolic and regulatory networks in these vital organelles in model plant systems, and furthermore, crop species, will be highly beneficial to modern agriculture.

PEROXISOME PROTEOMICS STUDIES IN PLANTS

Innovations in protein identification techniques coupled with high sensitivity instrumentation facilities have fueled the increased use of mass spectrometry-based proteomics to map subcellular (organelle) proteomes (Yates et al., 2005; Au et al., 2007; Yan et al., 2009; Wiederhold et al., 2010). Likewise, peroxisome proteomics have also been undertaken by various groups in diverse organisms encompassing yeasts, mammals, plants, and trypanosomes

(Colasante et al., 2006; Saleem et al., 2006). Given its completely sequenced and annotated genome and a wide suite of readily available molecular genetic resources, *Arabidopsis* was naturally the top choice for this approach to decipher the plant peroxisome proteome. However, early peroxisome proteome analysis in *Arabidopsis* was hindered by the lack of good peroxisome purification protocols. A combination of factors, such as the fragility of peroxisomes, elevated secondary metabolite levels in *Arabidopsis*, adherence of peroxisomes to mitochondria and chloroplasts, and the low peroxisome number in leaf mesophyll cells, made high purity isolation of *Arabidopsis* peroxisomes a challenging task. Thus, initial proteomic studies of *Arabidopsis* peroxisomes from greening and etiolated cotyledons only identified a small number of known and putative novel peroxisomal proteins (Fukao et al., 2002, 2003). The development of an isolation protocol for *Arabidopsis* leaf peroxisomes, which uses a two successive density gradient centrifugation method, resulted in the successful identification of 36 known peroxisome proteins and dozens of candidate novel proteins, some of which were later confirmed to be peroxisome localized (Reumann et al., 2007). A parallel large scale experiment, which used density centrifugation followed by free-flow electrophoresis, purified peroxisomes from *Arabidopsis* suspension cultured cells and discovered over 20 possible novel peroxisomal proteins by mass spectrometry (Eubel et al., 2008). Apart from *Arabidopsis*, soybean (*Glycine max*), and spinach (*Spinacia oleracea*) peroxisomes were also subjected to proteome analysis. About 30 peroxisomal proteins were identified from purified peroxisomes from etiolated cotyledons of soybean, among them is an adenine nucleotide transporter (Arai et al., 2008a,b). A few new peroxisomal proteins, including two enzymes in phylloquinone (vitamin K1) biosynthesis, were discovered by spinach leaf peroxisome proteomics (Babujee et al., 2010).

The NSF-funded *Arabidopsis* peroxisome 2010 project was initiated in late 2006 and is near its completion. The major goal for this project was to discover novel peroxisomal components and reveal new peroxisomal functions in *Arabidopsis*. Using one-dimensional gel electrophoresis (1-DE) followed by liquid chromatography and tandem mass spectrometry (LC-MS/MS), in-depth proteome analysis of three *Arabidopsis* peroxisomal subtypes, i.e., those from green leaves, etiolated germinating seedlings, and senescent leaves, respectively, was performed. Using fluorescence microscopy, the subcellular localization of over 100 putative novel peroxisomal proteins identified from proteomics and *in silico* PTS searches of the *Arabidopsis* genome was tested, and peroxisomal targeting for about 50 of them was confirmed (Reumann et al., 2009; Quan et al., unpublished). From leaves of 4-week-old plants, 85 known peroxisomal proteins were detected, and another 14 novel proteins were assigned to peroxisomes after subcellular targeting validations (Reumann et al., 2009; Quan et al., 2010). From peroxisomes of etiolated seedlings, another 15 novel peroxisomal proteins were discovered by proteomics combined with subcellular targeting assays (Quan et al., unpublished).

The recent proteomic studies followed by subcellular targeting verifications significantly expanded the list of *bona-fide* plant peroxisome proteins. Using data from published studies of plant peroxisomes, including the proteome analyses mentioned above, we have compiled a reference proteome for *Arabidopsis* peroxisomes (**Table 1**). For proteins identified by mass spectrometry-based experiments, we only included those that carry obvious PTS, unless they were later confirmed to be peroxisomal by a second approach, e.g., fluorescent protein subcellular targeting assay or genetic analysis. This list of *Arabidopsis* peroxisomal proteins currently stands at 163, which can be divided into the following categories: 117 PTS-containing matrix proteins, 38 membrane proteins, and eight proteins lacking recognizable PTS information. The 98 PTS1-containing proteins carry 23 diverse PTS1s, and the 19 PTS2-containing proteins harbor seven different PTS2s. Six proteins in the PTS2-containing protein category also bear C-terminal PTS1 or PTS1-like sequences.

SOME NOVEL ASPECTS OF PLANT PEROXISOMES REVEALED BY EXPERIMENTAL PROTEOMICS

Results from mass spectrometry-based proteomics studies in plants suggested novel metabolic and regulatory functions of peroxisomes in processes such as auxiliary β-oxidation, detoxification, nucleic acid metabolism, protein degradation, plant defense, and other metabolic processes (Kaur et al., 2009; Reumann, 2011). Several examples that represent plant-specific features of peroxisomes are described here. More examples can be found in a recent review (Reumann, 2011).

HISTIDINE TRIAD FAMILY

Histidine Triad (HIT) proteins belong to an evolutionarily conserved superfamily of nucleotide binding proteins whose defining feature is the H-φ-H-φ-H-φ-φ motif, where φ represents a hydrophobic amino acid. HIT proteins act as hydrolases or transferases on a multitude of nucleotide conjugate substrates (Brenner, 2002). The consequences of loss of HIT activity have various effects, from tumor formation in mammals, high temperature sensitive growth on galactose in yeast, to a reduction of bacterial growth in the presence of D-alanine (Bieganowski et al., 2002; Bardaweel et al., 2011; Martin et al., 2011), yet the exact roles for HIT proteins in these processes remain unclear. Animal HIT proteins have been reported to be cytosolic, nuclear, or mitochondrial (Huber and Weiske, 2008), and none was shown to be associated with peroxisomes. In contrast, three out of the five *Arabidopsis* HIT proteins (HIT1, 2, and 3) were detected in proteomics experiments (Reumann et al., 2007, 2009; Eubel et al., 2008) and later confirmed to be localized in peroxisomes (Reumann et al., 2009). HIT2 carries a characteristic PTS2, and the PTS1-like sequence on HIT1 (SKV>) and PTS2-like sequence on HIT3 (RVx_5HF) were later confirmed to be functional PTSs (Reumann et al., 2009; Quan et al., 2010). The occurrence of these proteins in peroxisomes appears to be a plant-specific phenomenon, as the *Arabidopsis* HIT PTSs are also conserved in their homologs in other plant species such as rice (**Table 1**). A recent *in vitro* study showed that most of the *Arabidopsis* HIT proteins can function as sulfohydrolases by catalyzing the conversion of adenosine 5′-phosphosulfate (APS) to AMP and sulfate (SO_4^{2-}; Guranowski et al., 2010). This study also showed that, in the presence of orthophosphate (P_i), HIT1/Hint4 exhibited APS phosphorylase activity as well, resulting in the formation of ADP. Moreover, this activity was determined to be pH dependent, with HIT1 exclusively (and more efficiently) catalyzing this reaction at acidic pHs. Considering their enzymatic activity,

Table 1 | Peroxisomal proteins in *Arabidopsis* and rice.

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
PTS-CONTAINING MATRIX PROTEINS						
ACH2	At1g01710	Acyl-CoA thioesterase	SKL	LOC_Os04g47120	PKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Tilton et al. (2000, 2004)
sT4	At1g04290	Thioesterase family protein	SNL	LOC_Os01g65950	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009)
KAT1	At1g04710	3-Ketoacyl-CoA thiolase 1	RQx$_5$HL	LOC_Os02g57260 LOC_Os10g31950	RQx$_5$HL RQx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Germain et al. (2001)
ACX3	At1g06290	Acyl-CoA oxidase 3	RAx$_5$HI/SSV	LOC_Os06g24704	RAx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Adham et al. (2005), Eastmond et al. (2000b), Froman et al. (2000), Rylott et al. (2003), Zolman et al. (2000)
ACX6	At1g06310	Acyl-CoA oxidase 6	RAx$_5$HI/SSL	LOC_Os11g39220	RLx$_5$HL	Adham et al. (2005)
ACD31.2	At1g06460	Small heat shock protein	RLx$_5$HF/PKL	no match		Ma et al. (2006)
NDA1	At1g07180	NADPH dehydrogenase A1	SRI	LOC_Os01g61410	SRI	Carrie et al. (2008)
UP6	At1g16730	Unknown protein 6	SKL	LOC_Os06g06630	CRL	Reumann et al. (2009), Quan et al. (2010)
4Cl3	At1g20480	4-Coumarate:CoA ligase 3	SKL	LOC_Os03g04000	SKL	Eubel et al. (2008), Shockey et al. (2003)
OPCL1	At1g20510	OPC-8:0 ligase 1	SKL	LOC_Os03g04000*	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Kienow et al. (2008), Koo et al. (2006)
AAE1	At1g20560	Acyl-activating enzyme 1	SKL	LOC_Os03g04130 LOC_Os03g04120 LOC_Os02g02700 LOC_Os01g24030	SKL SKL SKL SKL	Eubel et al. (2008), Reumann et al. (2009), Shockey et al. (2003)
CAT3	At1g20620	Catalase 3	QKL-10	LOC_Os03g03910 LOC_Os06g51150 LOC_Os02g02400	QKL-10 QKL-10 VKI-10	Eubel et al. (2008), Reumann et al. (2007, 2009), Du et al. (2008), Frederick and Newcomb (1969), Frugoli et al. (1996), Fukao et al. (2002, 2003), Zimmermann et al. (2006)
CAT1	At1g20630	Catalase 1	QKL-10	LOC_Os03g03910*	QKL-10	Eubel et al. (2008), Reumann et al. (2007, 2009), Du et al. (2008), Frederick and Newcomb (1969), Frugoli et al. (1996), Zimmermann et al. (2006)
ATF1	At1g21770	Acetyl transferase 1	SSI	LOC_Os04g35200	SSM	Reumann et al. (2007, 2009)
GGT1	At1g23310	Glutamate-glyoxylate aminotransferase 1	SKM	LOC_Os07g01760	SRM	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002), Igarashi et al. (2003), Liepman and Olsen (2003)
DEG15	At1g28320	Deg/HtrA protease	SKL	LOC_Os05g41810	SKI	Eubel et al. (2008), Helm et al. (2007), Schuhmann et al. (2008)
AAE14	At1g30520	Acyl-activating enzyme 14	SSL	LOC_Os08g03630	none	Babujee et al. (2010)
st1	At1g48320	Small thioesterase 1	AKL	LOC_Os03g48480 LOC_Os05g04660	SKL AKL	Reumann et al. (2009)
pxPfkB	At1g49350	PfkB-type carbohydrate kinase family protein	SML	LOC_Os05g09370	RMx$_5$HL	Eubel et al. (2008), Lingner et al. (2011)
NQR	At1g49670	NADH:quinone reductase	SRL	LOC_Os09g28570	AKL	Eubel et al. (2008), Reumann et al. (2007, 2009)
IndA	At1g50510	Indigoidine synthase A	RIx$_5$HL	LOC_Os08g39420	SAL	Eubel et al. (2008), Reumann et al. (2009)
ICDH	At1g54340	NADP-dependent isocitrate dehydrogenase	SRL	LOC_Os01g14580	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2003)

(Continued)

Table 1 | Continued

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
AAE18	At1g55320	Acyl-activating enzyme 18	SRI	LOC_Os03g59080	SKL	Shockey et al. (2003), Wiszniewski et al. (2009)
NS	At1g60550	Naphthoate synthase	RLx$_5$HL	LOC_Os01g47350	RLx$_5$HL	Reumann et al. (2007)
				LOC_Os02g43720	RAx$_5$HL	
ECI	At1g65520	Monofunctional enoyl CoA hydratase/isomerase c	SKL	LOC_Os05g45300*	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Goepfert et al. (2008)
PAO4	At1g65840	Polyamine oxidase 4	SRM	LOC_Os04g57550	CRT^	Eubel et al. (2008), Kamada-Nobusada et al. (2008), Ono et al. (2011)
				LOC_Os04g57560	SRL	
AAE12	At1g65890	Acyl-activating enzyme 12	SRL	LOC_Os09g38350	ARL	Shockey et al. (2003), Wiszniewski et al. (2009)
				LOC_Os03g03790	SRL	
				LOC_Os04g57850	SKM	
HPR	At1g68010	Hydroxypyruvate reductase 1	SKL	LOC_Os02g01150	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002), Mano et al. (1997), Pracharoenwattana et al. (2010)
GGT2	At1g70580	Glutamate-glyoxylate aminotransferase 2	SRM	LOC_Os07g01760*	SRM	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002), Igarashi et al. (2003), Liepman and Olsen (2003)
ECH2	At1g76150	Monofunctional enoyl-CoA hydratase 2	SSL	LOC_Os09g37280	SSL	Eubel et al. (2008), Reumann et al. (2007, 2009), Goepfert et al. (2006), Strader et al. (2011)
ATF2	At1g77540	Acetyltransferase	SSI	LOC_Os04g35200*	SSM	Reumann et al. (2009)
NADK3	At1g78590	NADH Kinase 3	SRY	LOC_Os09g17680	none	Waller et al. (2010)
OPR3	At2g06050	12-Oxophytodienoate reductase 3	SRL	LOC_Os08g35740	SRM	Eubel et al. (2008), Reumann et al. (2007, 2009), Sanders et al. (2000), Schaller et al. (2000), Stintzi and Browse (2000)
				LOC_Os02g35310	SPL	
SGAT1	At2g13360	Serine-glyoxylate aminotransferase	SRI	LOC_Os08g39300	SRI	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002), Liepman and Olsen (2003)
MDH1	At2g22780	NAD$^+$-malate dehydrogenase 1	RIx$_5$HL	LOC_Os12g43630	RMx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002, 2003), Cousins et al. (2008), Pracharoenwattana et al. (2007)
				LOC_Os03g56280	RIx$_5$HL	
Uri	At2g26230	Uricase	SKL	LOC_Os01g64520	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009)
st5	At2g29590	Small thioesterase 5	SKL	LOC_Os02g32200	SKL	Reumann et al. (2009)
				LOC_Os04g35590	SKL	
				LOC_Os01g12910	SKL	
NDA2	At2g29990	NADPH dehydrogenase A2	SRI	LOC_Os01g61410	SRI	Carrie et al. (2008)
CHYH1	At2g30650	ATP-dependent caseinolytic Clp protease/crotonase family protein	AKL	LOC_Os12g16350	PKL	Lingner et al. (2011)
				LOC_Os10g42210	PKL	
CHYH2	At2g30660	ATP-dependent caseinolytic Clp protease/crotonase family protein	AKL	LOC_Os12g16350*	PKL	Lingner et al. (2011)
				LOC_Os10g42210*	PKL	
UP3	At2g31670	Unknown protein	SSL	LOC_Os07g41810	ANL	Reumann et al. (2007, 2009)
				LOC_Os07g41820	ANL	
KAT2	At2g33150	3-Ketoacyl-CoA thiolase 2	RQx$_5$HL	LOC_Os02g57260*	RQx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Germain et al. (2001), Zolman et al. (2000), Fukao et al. (2003), Afitlhile et al. (2005), Castillo et al. (2004), Footitt et al. (2007a), Hayashi et al. (1998), Pye et al. (2010)
				LOC_Os10g31950*	RQx$_5$HL	

(Continued)

Table 1 | Continued

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
ACX5	At2g35690	Acyl-CoA oxidase 5	AKL	LOC_Os06g01390	SRL	Schilmiller et al. (2007)
GLH	At2g38180	GDSL motif lipase/ hydrolase family protein	ARL	LOC_Os06g36520	AML	Eubel et al. (2008)
PM16	At2g41790	Peptidase family M16	PKL	LOC_Os07g38260	MKL	Eubel et al. (2008), Reumann et al. (2009)
				LOC_Os07g38270	MKL	
				LOC_Os07g38280	MKL	
CuAO	At2g42490	Copper amine oxidase	SKL	LOC_Os04g40040	SKL	Eubel et al. (2008), Reumann et al. (2009)
CSY3	At2g42790	Citrate synthase 3	RLx$_5$HL/SSV	LOC_Os02g13840	RLx$_5$HL/SAL	Eubel et al. (2008), Reumann et al. (2007, 2009), Pracharoenwattana et al. (2005)
PAO2	At2g43020	Polyamine oxidase 2	SRL	LOC_Os04g53190	SRL	Kamada-Nobusada et al. (2008), Ono et al. (2011)
SO	At3g01910	Sulfite oxidase	SNL	LOC_Os08g41830	SKM	Eubel et al. (2008), Reumann et al. (2007, 2009),
				LOC_Os12g25630	SLL	Eilers et al. (2001), Lang et al. (2007)
SDRc	At3g01980	Short-chain dehydro-genase/reductase c	SYM	LOC_Os03g63290	SFM	Reumann et al. (2007, 2009), Lingner et al. (2011)
6PGDH	At3g02360	Phosphogluconate dehydrogenase	SKI	LOC_Os06g02144	AKM	Eubel et al. (2008), Reumann et al. (2007, 2009)
LACS6	At3g05970	Long-chain acyl-CoA synthetase 6	RIx$_5$HL	LOC_Os12g04990	RLx$_5$HL/PKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fulda et al. (2004)
IBR3	At3g06810	IBA-response 3	SKL	LOC_Os07g47820	ARM	Eubel et al. (2008), Reumann et al. (2009), Zolman et al. (2007, 2008)
MFP2	At3g06860	Fatty acid multi-functional protein 2	SRL	LOC_Os01g24680	ARL	Eubel et al. (2008), Reumann et al. (2007, 2009),
				LOC_Os05g06300	ARM	Arent et al. (2010), Eastmond and Graham (2000),
				LOC_Os05g29880	SRL	Richmond and Bleecker (1999), Rylott et al. (2006)
SDRb	At3g12800	Short-chain dehydro-genase/reductase b	SKL	LOC_Os04g52400	SKL	Eubel et al. (2008), Reumann et al. (2007)
HAOX1	At3g14150	Hydroxy-acid oxidase 1	SML	LOC_Os07g42440	SLL	Reumann et al. (2009)
				LOC_Os07g05820	SRL	
				LOC_Os03g57220	PRL	
				LOC_Os04g53210	SRL	
GO1	At3g14415	Glycolate oxidase 1	PRL	LOC_Os07g05820*	SRL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002)
GO2	At3g14420	Glycolate oxidase 2	ARL	LOC_Os07g05820*	SRL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002)
HBCDH	At3g15290	Hydroxybutyryl-CoA dehydrogenase	PRL	LOC_Os01g58380	SSL	Eubel et al. (2008), Reumann et al. (2007, 2009)
AAE7	At3g16910	Acyl-activating enzyme 7	SRL	LOC_Os03g19240	SRM	Eubel et al. (2008), Reumann et al. (2009), Shockey et al. (2003), Turner et al. (2005a)
				LOC_Os03g19250	SRM	
GPK1	At3g17420	Glyoxysomal protein kinase 1	AKI	LOC_Os01g21960	SSK	Fukao et al. (2003), Ma and Reumann (2008)
SCO3	At3g19570	Snowy Cotyledon 3	SRL	LOC_Os03g10820	none	Albrecht et al. (2010)
ICL	At3g21720	Isocitrate lyase	SRM	LOC_Os07g34520	SRM	Fukao et al. (2003), Eastmond et al. (2000a), Olsen et al. (1993)
GR1	At3g24170	Glutathione reductase 1	TNL	LOC_Os02g56850	TNL	Eubel et al. (2008), Reumann et al. (2007), Kataya and Reumann (2010)
BADH	At3g48170	Aldehyde dehydrogenase	SKL	LOC_Os08g32870	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009),
				LOC_Os04g39020	SKL	Mitsuya et al. (2009)
MIF	At3g51660	Macrophage migration inhibitory factor	SKL	LOC_Os11g01600	none	Reumann et al. (2007), Reumann et al. (2009), Li et al. (2009)

(Continued)

Table 1 | Continued

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
ACX4	At3g51840	Acyl-CoA oxidase 4	SRL	LOC_Os01g06600 LOC_Os05g07090 LOC_Os06g23780	ARL SRL ARL	Eubel et al. (2008), Reumann et al. (2007, 2009), Rylott et al. (2003), Zolman et al. (2000), Hayashi et al. (1999)
MDAR1	At3g52880	Monodehydroascorbate reductase 1	AKI	LOC_Os09g39380 LOC_Os08g44340	SKI AKV	Eubel et al. (2008), Reumann et al. (2007, 2009), Lisenbee et al. (2005)
SDR	At3g55290	Short-chain dehydrogenase/reductase	SSL	LOC_Os08g39960	SSL	Eubel et al. (2008), Reumann et al. (2007, 2009)
ZnDH	At3g56460	Zinc-binding dehydrogenase	SKL	LOC_Os05g24880	SRL	Eubel et al. (2008), Reumann et al. (2009)
HIT3	At3g56490	Histidine triad family protein 3	RVx$_5$HF	LOC_Os01g59750 LOC_Os11g18990	RLx$_5$HL RLx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Quan et al. (2010), Guranowski et al. (2010)
CP	At3g57810	Cysteine protease	SKL	LOC_Os09g31280	SRL	Lingner et al. (2011)
CSY2	At3g58750	Citrate synthase 2	RLx$_5$HL/SAL	LOC_Os02g13840*	RLx$_5$HL/SAL	Eubel et al. (2008), Reumann et al. (2009), Pracharoenwattana et al. (2005)
PAO3	At3g59050	Polyamine oxidase 3	SRM	LOC_Os04g53190*	SRL	Kamada-Nobusada et al. (2008), Ono et al. (2011), Moschou et al. (2008)
st3	At3g61200	Small thioesterase 3	SKL	LOC_Os07g27960	ASL	Eubel et al. (2008), Reumann et al. (2009), Fukao et al. (2003)
ACH	At4g00520	Acyl-CoA thioesterase family protein	AKL	LOC_Os04g47120*	PKL	Eubel et al. (2008)
EH3	At4g02340	Epoxide hydrolase 3	ASL	LOC_Os05g19150 LOC_Os01g15120 LOC_Os03g61340 LOC_Os10g35520	AEM SKF SRL RQx$_4$HL	Eubel et al. (2008), Reumann et al. (2007, 2009)
MCD	At4g04320	Malonyl-CoA decarboxylase	SRL	LOC_Os09g23070	none	Eubel et al. (2008), Reumann et al. (2009), Carrie et al. (2009)
4CL1	At4g05160	4-Coumarate:CoA ligase 1	SKM	LOC_Os03g05780 LOC_Os10g42800 LOC_Os07g17970	SKL SRL SRL	Eubel et al. (2008), Reumann et al. (2007, 2009), Kienow et al. (2008), Schneider et al. (2005)
IBR1	At4g05530	Indole-3-butyric acid response 1	SRL	LOC_Os09g04730	SRL	Eubel et al. (2008), Reumann et al. (2007, 2009), Wiszniewski et al. (2009), Zolman et al. (2008)
IBR10	At4g14430	Indole-3-butyric acid response 10	PKL	LOC_Os05g45300	SKL	Reumann et al. (2007, 2009), Goepfert et al. (2008), Zolman et al. (2008)
ECHIA	At4g16210	Monofunctional enoyl-CoA hydratase/isomerase a	SKL	LOC_Os03g19680	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009)
HIT1	At4g16566	Histidine triad family protein 1	SKV	LOC_Os01g59750*	RLx$_5$HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Guranowski et al. (2010)
ACX1	At4g16760	Acyl-CoA oxidase 1	ARL	LOC_Os06g01390*	SRL	Eubel et al. (2008), Reumann et al. (2009), Adham et al. (2005), Castillo et al. (2004), Schilmiller et al. (2007), Hooks et al. (1999), Pinfield-Wells et al. (2005)
GO3	At4g18360	Glycolate oxidase 3	AKL	LOC_Os03g57220*	PRL	Eubel et al. (2008), Reumann et al. (2007, 2009)
4Cl5	At4g19010	4-Coumarate:CoA ligase 5	SRL	LOC_Os08g04770	SKL	Shockey et al. (2003)
NDB1	At4g28220	NADPH dehydrogenase B1	SRI	LOC_Os06g47000 LOC_Os05g26660	SRI SSL	Carrie et al. (2008)
AIM1	At4g29010	Abnormal inflorescence meristem 1	SKL	LOC_Os02g17390	SRM	Eubel et al. (2008), Reumann et al. (2009), Richmond and Bleecker (1999), Delker et al. (2007)

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Table 1 | Continued

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
CAT2	At4g35090	Catalase 2	QKL-10	LOC_Os03g03910*	QKL-10	Eubel et al. (2008), Reumann et al. (2007, 2009), Frederick and Newcomb (1969), Frugoli et al. (1996), Fukao et al. (2002), Zimmermann et al. (2006)
AGT2	At4g39660	Alanine: glyoxylate aminotransferase 2	SRL	LOC_Os03g07570	SGL	Liepman and Olsen (2003)
				LOC_Os03g21960	SKL	
				LOC_Os05g39770	SKL	
MLS	At5g03860	Malate synthase	SRL	LOC_Os04g40990	CKL	Fukao et al. (2003), Olsen et al. (1993), Cornah et al. (2004)
BIOTIN F	At5g04620	7-Keto-8-aminopelargonic acid synthase	PKL	LOC_Os01g53450	SKL	Tanabe et al. (2011)
				LOC_Os10g41150	SKL	
MDH2	At5g09660	NAD^+-malate dehydrogenase 2	RIx_5HL	LOC_Os12g43630*	RMx_5HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Cousins et al. (2008), Pracharoenwattana et al. (2007)
				LOC_Os03g56280*	RIx_5HL	
ASP3	At5g11520	Aspartate aminotransferase	RIx_5HL	LOC_Os01g55540	RLx_5HL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2002), Mettler and Beevers (1980), Schultz and Coruzzi (1995)
ELT1	At5g11910	Esterase/lipase/ thioesterase family 1	SRI	LOC_Os01g39790	SSA	Reumann et al. (2009)
				LOC_Os05g46210	PKL	
AAE5	At5g16370	Acyl-activating enzyme 5	SRM	LOC_Os04g57850*	SKM	Eubel et al. (2008), Reumann et al. (2007, 2009), Shockey et al. (2003)
ATMS1	At5g17920	Cobalamin-independent methionine synthase	SAK	LOC_Os12g42884	SAK	Reumann et al. (2007), Reumann et al. (2009)
CSD3	At5g18100	Copper/zinc superoxide dismutase 3	AKL	LOC_Os03g11960	SAV	Eubel et al. (2008), Reumann et al. (2007, 2009), Kliebenstein et al. (1998)
NUDT19	At5g20070	Nudix hydrolase homolog 19	SSL	LOC_Os06g04910	SNL	Babujee et al. (2010)
AAE17	At5g23050	Acyl-activating enzyme 17	SKL	LOC_Os09g21230	SKI	Eubel et al. (2008), Reumann et al. (2009), Shockey et al. (2003)
MIA40	At5g23395	Mitochondrial inter-membrane space assembly machinery 40	SKL	LOC_Os04g44550	PKL	Carrie et al. (2010)
6PGL	At5g24400	6-Phosphoglu conolactonase	SKL	LOC_Os08g43370	SSI	Reumann et al. (2007)
LACS7	At5g27600	Long-chain acyl-CoA synthetase 7	RLx_5HI/SKL	LOC_Os11g04980	RLx_5HL/SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Fulda et al. (2004)
AtHsp15.7	At5g37670	Heat shock protein similar to 17.6 kDa class I	SKL	LOC_Os06g14240	SKL	Ma et al. (2006)
GSTT1	At5g41210	Glutathione S-transferase θ isoform 1	SKI	LOC_Os11g37730	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Dixon et al. (2009)
				LOC_Os11g37750	SKL	
SCP2	At5g42890	Sterol carrier protein 2	SKL	LOC_Os02g52720	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Edqvist et al. (2004), Zheng et al. (2008)
AtDCI	At5g43280	Δ3,5-Δ2,4-Enoyl-CoA-isomerase	AKL	LOC_Os01g70090	SKL	Eubel et al. (2008), Reumann et al. (2007, 2009), Goepfert et al. (2005)
UP5	At5g44250	Unknown protein 5	SRL	LOC_Os11g40070	SKL	Reumann et al. (2009)

(Continued)

Table 1 | Continued

Gene name	At locus	Annotation	At PTS	Os locus	Os PTS	Reference
LON2	At5g47040	Lon protease homolog 2	SKL	LOC_Os09g36300	SKL	Reumann et al. (2009), Lingard and Bartel (2009)
ACAT1.3	At5g47720	Acetoacetyl-CoA thiolase 1.3	SAL	LOC_Os01g02020	SSL	Carrie et al. (2007)
HIT2	At5g48545	Histidine triad family protein 2	RLx_5HL	LOC_Os11g18990* LOC_Os12g13120	RLx_5HL RLx_5HL	Reumann et al. (2009), Guranowski et al. (2010)
KAT5	At5g48880	3-Ketoacyl-CoA thiolase 5	RQx_5HL	LOC_Os02g57260*	RQx_5HL	Reumann et al. (2007, 2009), Germain et al. (2001), Castillo et al. (2004)
TLP	At5g58220	Transthyretin-like protein	$RLx_5HL^{\#}$	LOC_Os03g27320	$RMx_5HL^{\#}$	Eubel et al. (2008), Reumann et al. (2007, 2009), Lamberto et al. (2010)
4CL2	At5g63380	4-Coumarate:CoA ligase 2	SKL	LOC_Os01g67540	SRL	Reumann et al. (2009), Kienow et al. (2008), Schneider et al. (2005)
ACX2	At5g65110	Acyl-CoA oxidase 2	RIx_5HL	LOC_Os11g39220*	RIx_5HL	Eubel et al. (2008), Reumann et al. (2009), Adham et al. (2005), Hooks et al. (1999)
UP7	At5g65400	Unknown protein 7	SLM	LOC_Os04g37710	none	Reumann et al. (2009)
CHY1	At5g65940	3-Hydroxyisobutyryl-CoA hydrolase	AKL	LOC_Os12g16350	PKL	Eubel et al. (2008), Reumann et al. (2009), Lange et al. (2004), Zolman et al. (2001a)

Gene name	At locus	Annotation	Os locus	Reference
PEROXISOME MEMBRANE PROTEINS				
PEX11c	At1g01820	Peroxin 11 c	LOC_Os06g03660	Lingard et al. (2008), Lingard and Trelease (2006), Orth et al. (2007), Nito et al. (2007)
PEX6	At1g03000	Peroxin 6	LOC_Os04g52690	Delker et al. (2007), Zolman and Bartel (2004)
PEX7	At1g29260	Peroxin 7	LOC_Os02g14790	Hayashi et al. (2005), Ramon and Bartel (2011), Singh et al. (2009), Woodward and Bartel (2005)
PEX11a	At1g47750	Peroxin 11a	LOC_Os03g19010 LOC_Os03g19000	Lingard et al. (2008), Lingard and Trelease (2006), Orth et al. (2007)
PEX3B	At1g48635	Peroxin 3 isoform B	LOC_Os09g14510	Nito et al. (2007), Hunt and Trelease (2004)
PEX2	At1g79810	Peroxin 2	LOC_Os05g19480	Nito et al. (2007), Hu et al. (2002), Prestele et al. (2010), Sparkes et al. (2005)
DRP3B	At2g14120	Dynamin-related protein 3B	LOC_Os01g69130 LOC_Os04g31190	Arimura et al. (2004), Arimura and Tsutsumi (2002), Fujimoto et al. (2009), Zhang and Hu (2009)
PEX10	At2g26350	Peroxin 10	LOC_Os07g41800	Nito et al. (2007), Prestele et al. (2010), Flynn et al. (2005), Schumann et al. (2003, 2007), Sparkes et al. (2003)
PEX16	At2g45690	Peroxin 16	LOC_Os02g03070	Nito et al. (2007), Karnik and Trelease (2005, 2007), Lin et al. (1999, 2004)
PEX11d	At2g45740	Peroxin 11d	LOC_Os03g02590	Lingard et al. (2008), Lingard and Trelease (2006), Orth et al. (2007)
PEX19A	At3g03490	Peroxin 19 isoform A	LOC_Os02g44220	Nito et al. (2007), Hadden et al. (2006)
PEX12	At3g04460	Peroxin 12	LOC_Os10g32960	Nito et al. (2007), Prestele et al. (2010), Fan et al. (2005), Mano et al. (2006)
PEX13	At3g07560	Peroxin 13	LOC_Os07g05810	Nito et al. (2007), Mano et al. (2006), Boisson-Dernier et al. (2008)
APEM9	At3g10572	Aberrant peroxisome morphology 9	LOC_Os06g48970	Goto et al. (2011)
PEX3A	At3g18160	Peroxin 3 isoform A	LOC_Os09g14510*	Nito et al. (2007), Hunt and Trelease (2004)
DRP5B	At3g19720	Dynamin-related protein 5B	LOC_Os12g07880	Zhang and Hu (2010)
PEX22	At3g21865	Peroxin 22	LOC_Os04g53690 LOC_Os04g57680	Lingard et al. (2009), Zolman et al. (2005)
PEX11b	At3g47430	Peroxin 11b	LOC_Os04g45210	Lingard and Trelease (2006), Orth et al. (2007), Desai and Hu (2008)

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Gene name	At locus	Annotation	Os locus	Reference
FIS1A	At3g57090	Fission 1 isoform A	LOC_Os03g24060 LOC_Os05g31770 LOC_Os01g72280	Delker et al. (2007), Zheng et al. (2008), Lingard et al. (2008), Zhang and Hu (2009), Scott et al. (2006)
PEX11e	At3g61070	Peroxin 11e	LOC_Os06g03660*	Lingard et al. (2008), Lingard and Trelease (2006), Orth et al. (2007)
DRP3A	At4g33650	Dynamin-related protein 3A	LOC_Os01g69130* LOC_Os04g31190*	Arimura et al. (2004), Fujimoto et al. (2009), Zhang and Hu (2009), Mano et al. (2004)
PEX1	At5g08470	Peroxin 1	LOC_Os08g44240	Nito et al. (2007), Charlton et al. (2005)
FIS1B	At5g12390	Fission 1 isoform B	LOC_Os05g31770* LOC_Os01g72280* LOC_Os03g24060*	Zheng et al. (2008), Lingard et al. (2008), Zhang and Hu (2009)
PEX19B	At5g17550	Peroxin 19 isoform B	LOC_Os02g44220*	Nito et al. (2007), Hadden et al. (2006)
PEX4	At5g25760	Peroxin 4	LOC_Os02g42314	Nito et al. (2007), Lingard et al. (2009), Zolman et al. (2005)
PEX5	At5g56290	Peroxin 5	LOC_Os08g39080	Hayashi et al. (2005), Ramon and Bartel (2011), Woodward and Bartel (2005), Brown et al. (2011); Khan and Zolman (2010)
PEX14	At5g62810	Peroxin 14	LOC_Os05g01090	Eubel et al. (2008), Reumann et al. (2007, 2009), Hayashi et al. (2000), Nito et al. (2002)
PNC1	At3g05290	Peroxisomal adenine nucleotide carrier 1	LOC_Os05g32630	Eubel et al. (2008), Arai et al. (2008a), Linka et al. (2008)
CDC	At3g55640	Ca^{2+}-dependent carrier	LOC_Os03g16080 LOC_Os01g04990	Carrie et al. (2009)
PMD1	At3g58840	Peroxisomal and Mitochondrial Division Factor 1	no match	Aung and Hu (2011)
PMP22	At4g04470	Peroxisomal membrane protein of 22 kDa	LOC_Os02g13270 LOC_Os08g45210 LOC_Os01g12800	Eubel et al. (2008), Murphy et al. (2003), Tugal et al. (1999)
PXA1/CTS	At4g39850	Peroxisomal ABC transporter 1/Comatose	LOC_Os01g73530 LOC_Os05g01700	Eubel et al. (2008), Reumann et al. (2009), Footitt et al. (2002), Hayashi et al. (2002), Hooks et al. (2007), Kunz et al. (2009), Nyathi et al. (2010), Theodoulou et al. (2005), Zhang et al. (2011), Zolman et al. (2001b)
PNC2	At5g27520	Peroxisomal adenine nucleotide carrier 2	LOC_Os05g32630*	Eubel et al. (2008), Arai et al. (2008a), Linka et al. (2008)
PXN/PMP38/ PMP36	At2g39970	Peroxisomal membrane protein of 36 kDa	LOC_Os03g15860 LOC_Os02g13170 LOC_Os09g33470	Eubel et al. (2008), Reumann et al. (2009), Bernhardt et al. (2011), Fukao et al. (2001)
PEN2	At2g44490	Penetration 2	LOC_Os06g21570 LOC_Os04g39880 LOC_Os04g39900	Bednarek et al. (2009), Clay et al. (2009), Lipka et al. (2005), Westphal et al. (2008), Maeda et al. (2009)
MDAR4	At3g27820	Monodehydroascorbate reductase 4	LOC_Os02g47800 LOC_Os02g47790	Reumann et al. (2009), Lisenbee et al. (2005), Eastmond (2007)
APX3	At4g35000	Ascorbate peroxidase 3	LOC_Os08g43560 LOC_Os04g14680	Eubel et al. (2008), Reumann et al. (2007, 2009), Fukao et al. (2003), Fukao et al. (2002), Lisenbee et al. (2003), Narendra et al. (2006)
DHAR	At1g19570	Dehydroascorbate reductase 1	LOC_Os05g02530 LOC_Os06g12630	Reumann et al. (2009)
PEROXISOME PROTEINS LACKING PTS				
GLX1	At1g11840	Glyoxylase I homolog	LOC_Os08g09250	Reumann et al. (2009), Quan et al. (2010)
SMP2	At2g02510	Short membrane protein 2	LOC_Os02g35610	Abu-Abied et al. (2009)
SOX	At2g24580	Sarcosine oxidase	LOC_Os09g32290 LOC_Os12g35890 LOC_Os01g21380	Goyer et al. (2004)
CoAE	At2g27490	Dephospho-CoA kinase	LOC_Os01g25880	Reumann et al. (2009)

(Continued)

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Gene name	At locus	Annotation	Os locus	Reference
B12D1	At3g48140	Senescence-associated protein/B12D-related protein	LOC_Os07g17330 LOC_Os07g17310 LOC_Os06g13680	Reumann et al. (2009)
NDPK1	At4g09320	Nucleoside diphosphate kinase type 1	LOC_Os10g41410	Reumann et al. (2009)
CPK1	At5g04870	Calcium dependent protein kinase 1	LOC_Os12g30150 LOC_Os07g06740 LOC_Os03g57450	Coca and San Segundo (2010)
ACAT2	At5g48230	Acetoacetyl-CoA thiolase 2	LOC_Os09g07830	Reumann et al. (2007, 2009)

**Loci that have already been listed once; #internal PTS2; ^proven localization; QKL (–10) in catalases are positioned 10 amino acids from the C-terminus.*

it is possible that the three peroxisomal HIT proteins are involved in recycling the pool of adenosine nucleotides in the peroxisome. Based on the pH specific activity of HIT1, we speculate that this protein may serve to buffer peroxisomal pH. Phenotypic and functional characterization of these HIT proteins will be needed to address their role in the peroxisome and in plant physiology.

PEROXISOMAL NADPH PRODUCTION

Many peroxisomal enzymes consume NADPH during reductive reactions. For instance, several enzymes involved in JA biosynthesis (OPR3), auxiliary β-oxidation (ECRs, SDRa), and detoxification (MDAR, GR, NQR), require NADPH for their activity, underscoring the critical need for this cofactor in the peroxisome (Nyathi and Baker, 2006; Kaur et al., 2009). Several NADPH dehydrogenases are also found in the peroxisome (Carrie et al., 2008). To maintain optimal activities of these enzymes, the diminishing NADPH pool needs to be continuously replenished. In addition to providing reducing equivalents, NAPDH is also essential in oxidative damage response and peroxisome protein import (Juhnke et al., 1996; Pool et al., 1998; Pollak et al., 2007).

In plants, the plastid localized oxidative pentose phosphate pathway (OPPP) is a primary source of NADPH. OPPP consists of a three-enzyme cascade comprising of glucose-6-phosphate dehydrogenase (G6PD), 6-phosphogluconolactonase (6PGL), and 6-phosphogluconate dehydrogenase (6PGDH). These enzymes act sequentially to convert glucose-6-phosphate to ribose-5-phosphate with the concomitant production of NADPH (Kruger and von Schaewen, 2003). Besides the OPPP, NADPH is also generated by NADP-dependent isocitrate dehydrogenase (ICDH), malic enzyme (ME), aldehyde dehydrogenase (ALDH), and NAD kinase (NADK; Pollak et al., 2007). Some earlier studies indicated that the NADPH generating enzymes in OPPP and ICDH are compartmentalized in plant peroxisomes (Donaldson, 1982; Corpas et al., 1998; del Rio et al., 2002; Mateos et al., 2003). In yeasts, the presence of peroxisomal ICDH is also necessary for β-oxidation of unsaturated fatty acids and NADPH is critical to dissipate H_2O_2 (Henke et al., 1998; van Roermund et al., 1998; Minard and McAlister-Henn, 1999). *Arabidopsis* peroxisome proteomics studies detected ICDH and 6PGDH and subcellular targeting studies validated their peroxisomal localization (Fukao et al., 2002, 2003; Reumann et al., 2007, 2009; Eubel et al., 2008). Although not identified in proteomics experiments, 6PGL was shown to be a dual localized protein carrying an N-terminal transit peptide directing it to chloroplasts and a C-terminal PTS1 targeting it to peroxisomes (Reumann et al., 2007). Interestingly, although the chloroplast targeting of 6PGL is indispensable for viability, plants were unaffected in the absence of a peroxisome localized isoform (Xiong et al., 2009), strengthening the notion that plant peroxisomes have alternative sources for NADPH generation. The only enzyme missing from the set of peroxisomal OPPP was recently found to be the plastidic G6PD1, which was selectively recruited to the peroxisomes under conditions that promote transient oxidation events. This study further demonstrated the cysteine dependent heterodimer formation between the plastid targeted G6PD1 isoform and a catalytically inactive isoform G6PD4, and the import of this heterodimer into peroxisomes (Meyer et al., 2011). As such, peroxisomes seem to have a complete set of OPPP enzymes.

De novo biosynthesis of NADPH also occurs in peroxisomes by the preferential phosphorylation of NADH by NADK3 (Turner et al., 2005a,b). Though not found in proteomics studies, NADK3 has been localized to peroxisomes via a novel PTS1, SRY> (Waller et al., 2010). Lastly, ALDHs are classified as NADP-dependent enzymes that detoxify aldehyde substrates (Kirch et al., 2004). Mammals possess multiple isoforms of ALDHs, which were found to be induced by oxidative stress; one particular isoform was linked to the prevention of oxidative damage (Pappa et al., 2003; Vasiliou and Nebert, 2005). Peroxisome proteomic analysis in *Arabidopsis* has repeatedly identified an ALDH, BADH, which has a putative role in polyamine degradation (Reumann et al., 2007, 2009; Eubel et al., 2008). Whether this protein contributes to the maintenance of peroxisomal redox homeostasis/NADP turnover needs to be ascertained. Thus, plant peroxisomes seem to have several routes to maintain a supply of NADPH within the organelle, possibly as a countermeasure for the dangers posed by oxidative stress emanating from unchecked/continuous H_2O_2 generated within the peroxisome.

METABOLITE TRANSPORTERS

Proteomic analysis of the soybean peroxisomal membrane proteins led to the identification of a soybean peroxisomal adenine nucleotide transporter and later on two homologous proteins (PNC1, PNC2) from *Arabidopsis* (Arai et al., 2008b). An

independent study of peroxisome membrane proteins isolated from *Arabidopsis* suspension cultured cells also identified PNC2 as a novel constituent of the peroxisome membrane (Eubel et al., 2008). A bioinformatics based approach followed by cell biological and biochemical validations found PNC1 and PNC2 as adenine nucleotide transporters in *Arabidopsis* as well (Linka et al., 2008). Consistent with the ATP transporter activity of the PNCs, their RNAi lines were sucrose dependent for seedling establishment and impaired in post-germinative lipid mobilization. Functional analysis of the PNCs highlights the critical need for ATP within peroxisomes and reinforces the notion that these proteins are the sole purveyors of ATP transport into peroxisomes (Arai et al., 2008b; Linka et al., 2008).

PMP38/PXN, like the PNCs, is also a member of the mitochondrial carrier family. It was initially identified as an integral peroxisome membrane protein in pumpkin cotyledons and considered to be a potential ATP/ADP transporter (Fukao et al., 2001). The presence of PMP38 in *Arabidopsis* peroxisomes was subsequently detected in isolated peroxisomes from proteomics works using suspension cultured cells and adult leaves (Eubel et al., 2008; Reumann et al., 2009). However, this protein failed to complement a yeast adenine nucleotide mutant (Linka et al., 2008) but instead was found to serve as an NAD^+ carrier involved in peroxisomal β-oxidation (Bernhardt et al., 2011).

PEROXISOME PROTEINS LACKING PTS

Dehydroascorbate reductase (DHAR) is part of the peroxisomal ascorbate-glutathione (PAG) cycle, which encompasses the enzymes MDAR1, MDAR4, APX3, and glutathione reductase (GR) and plays a key role in antioxidant metabolism (Kaur et al., 2009). DHAR was found to be peroxisomal in pea and tomato (Jimenez et al., 1997; Mittova et al., 2003), but was missing from the *Arabidopsis* PAG pathway until its proteomic identification and subcellular localization validation (Reumann et al., 2009). Glyoxylase I (GLXI) is another protein without obvious PTS identified from the leaf peroxisome proteome (Reumann et al., 2009). GLX system disposes of toxic byproducts such as methylglyoxal in two consecutive steps catalyzed by GLXI and GLXII (Mannervik, 2008; Yadav et al., 2008; Inoue et al., 2011). The verification of GLXI in the peroxisome expanded the suite of detoxification related proteins found in the peroxisome and indicated that half of the GLX pathway is compartmentalized in peroxisomes in *Arabidopsis* (Quan et al., 2010).

The plant-specific, senescence-associated *B12D* gene encodes for a small protein lacking any recognizable PTS. It was only detected in the proteome of leaf peroxisomes, and as a C-terminal YFP fusion was found to target to peroxisomes (Reumann et al., 2009). *B12D* genes in monocots such as barley and wheat are expressed during seed development but cease to be transcribed at seed maturity (Aalen et al., 1994, 2001; McIntosh et al., 2007). The germinating seed is purported to induce the expression of these genes *via* a putative gibberellic acid (GA) responsive promoter element. Consistent with this notion, the expression of this gene was found to be induced by GA but suppressed by abscisic acid (ABA; Steinum et al., 1998). Although no function has been attributed to B12D, the gene expression pattern suggests its role in seed germination/dormancy.

Dephospho-CoA kinase (CoAE) was identified in leaf peroxisome proteomics and localized to the periphery of the peroxisome membrane as a YFP fusion (Reumann et al., 2009). Coenzyme A (CoA) and derivatives thereof are the major currency behind many cellular metabolic pathways. CoA biosynthesis is accomplished in five successive enzymatic steps, the last of which is carried out by CoAE (Leonardi et al., 2005). Though the *in planta* effects of some of the enzymes catalyzing the preceding steps in CoA biosynthesis have been studied, the physiological role of CoAE in plants has not been analyzed (Rubio et al., 2006, 2008; Tilton et al., 2006). Given the number of β-oxidation reactions that require CoA, it will be necessary to determine the effect of CoAE on peroxisome metabolism.

Nucleoside diphosphate kinase type 1 (NDPK1) was another unexpected peroxisomal protein to be found through proteomics, and was seen to localize to peroxisomes as well as the cytosol and nucleus (Reumann et al., 2009). This multi-localization is perhaps not so surprising in light of the even more promiscuous localization reported for the mammalian NDPKs (Bosnar et al., 2009). NDPKs catalyze the interconversion of nucleoside diphosphates by transferring the phosphate group from a nucleoside triphosphates (NTP) to any other nucleoside diphosphates (NDP) except for ADP (Yegutkin, 2008). In view of this, NDPK1 might serve to regulate the concentration of different nucleotide phosphates within the peroxisome.

PEROXISOME PROTEOME IN RICE

THE NEED TO STUDY PEROXISOMES IN THE MONOCOT CROP PLANT, RICE

The pivotal roles of peroxisomes in plant development and stress responses make it highly necessary to study these organelles in crop plants, with the goal to improve the quality and yield of crop species. Rice (*Oryza sativa*) is one the three major staple food crops in the world and a model system for basic research in monocot plants. Traditionally, plant peroxisome studies have mainly focused on dicot species such as cucumber, pumpkin, watermelon, and pea (Beevers, 1979), and lately, *Arabidopsis* (Kaur et al., 2009); however, very little research has been carried out with these organelles in monocots, which differ significantly from dicots in architecture and physiology. Having a completely sequenced and well annotated genome, well developed transformation methods, and rich genetic and mutant resources, rice is deemed to be the logical choice for a model system to study peroxisome functions in monocot plants.

Despite the fact that rice has a larger genome than *Arabidopsis*, the advantages of studying rice orthologs of *Arabidopsis* genes have been exemplified by a number of cases, in which mutant phenotypes were revealed in rice but not in *Arabidopsis* mutant due to functional redundancy among gene family members in the latter. The best example is the identification of the gibberellin receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1) from rice, in which the *gid1* mutant shows a strong GA insensitive dwarf phenotype (Ueguchi-Tanaka et al., 2005). In contrast, three GID1 homologs exist in *Arabidopsis* and as a result, phenotypes could only be shown in higher order mutants whereas single mutant is indistinguishable from the wild-type plants (Griffiths et al., 2006). T-DNA insertion mutants for many of the new peroxisome genes

we recently identified have no apparent phenotypes (Cassin and Hu, unpublished). Studying mutants of their orthologs in rice may be an easier way to decipher the functions of some of these proteins.

Studying peroxisomes in rice may also have applications in engineering the more efficient C_4 photosynthetic pathway into C_3 crops for yield increase. Rice is a C_3 plant growing in warm environment, which favors photorespiration and thus reduces photosynthesis. However, in rice cells chloroplasts and stromules occupy 95% of the cell periphery, whereas peroxisomes and mitochondria, players in photorespiration, are present in the interior of the cell and lined up along the chloroplast walls (Sage and Sage, 2009). This interesting anatomy of rice mesophyll cells, which is atypical for a C_3 plant, was suggested to be significant in scavenging photorespiratory CO_2 to enhance the carboxylation capability of Rubisco for CO_2 refixation. In C_3 plants, peroxisomes were found to be responsible for the vast majority of the H_2O_2 produced during photorespiration (Foyer and Noctor, 2003). It would be interesting to investigate whether there are any changes to the activity of rice peroxisomal photorespiratory enzymes in association with these organelle rearrangements.

IN SILICO ANALYSIS OF THE RICE PEROXISOME PROTEOME

As a first step toward exploring the peroxisome proteome in cereal crop species, we performed an *in silico* analysis of the rice peroxisome proteome by searching the rice genome for proteins with sequence similarities with the *Arabidopsis* peroxisomal proteins (**Table 1**). Remarkably, with the exception of two proteins, every *Arabidopsis* peroxisome protein seems to have at least one homolog in rice. One exception is ACD31.2, a small heat shock protein. It is interesting that this protein as well as its PTS2 peptide are well conserved in most plant species (Ma et al., 2006) but entirely missing from rice. Another protein without an apparent homolog in rice is peroxisome and mitochondrial division factor 1 (PMD1), a plant-specific dual localized membrane protein involved in the proliferation of peroxisomes and mitochondria in *Arabidopsis* (Aung and Hu, 2011). Altogether, the putative rice peroxisome proteome consists of 133 matrix proteins, 47 membrane proteins, and 14 proteins with no apparent PTSs. Among the candidate peroxisome matrix proteins in rice, most proteins contain PTS1 or PTS2-like sequences just like their *Arabidopsis* counterparts, suggesting that these proteins are highly likely to be peroxisomal. Proteins which appear to have lost PTS1 signal include snowy cotyledon3 (SCO3), the dual localized malonyl-CoA decarboxylase (MCD; Carrie et al., 2008), a protein of unknown function (UP7), NADK3 (Waller et al., 2010), AAE14 (Babujee et al., 2010), and macrophage migration inhibitory factor, MIF (Li et al., 2009). Despite having a C-terminal PTS1, *Arabidopsis* SCO3 is actually localized to the periphery of peroxisomes and influences plastid development possibly through interaction with the cytoskeleton (Albrecht et al., 2010). Hence, the loss of the matrix targeting signal PTS1 in its rice homolog is not that surprising. For proteins whose homologs in *Arabidopsis* contain dual PTSs, CSY2 and LACS7 homologs retain the same PTSs, LACS6 gains a PTS1 (PKL>), ACX3 and ACX6 both lose their PTS1s, while ACD31.2 does not have an apparent rice homolog.

Rice appears to employ a greater diversity of PTSs, with (potentially) 37 assorted PTS1s and 5 PTS2s. Recognition of PTS1 in plants seems fairly plastic and tolerant of non-canonical substitutions (Lingner et al., 2011). These new PTS1s in rice still need to be validated *in planta* as genuine PTSs. An outright observation is the frequent substitution to Methionine (M) in both PTSs, i.e., at position 3 in the PTS1 in lieu of L or position 2 in PTS2 in lieu of L/I. Examples include ATF, OPR3, AAE7, AAE12, SO, 6PGDH, MFP2, and IBR3 for PTS1 and MDH and TLP for PTS2. Another interesting observation is the change of PTSs in the orthologs. For example, for the two proteins predicted to work sequentially in the pseudouridine catabolism pathway, i.e., Indigoidine synthase A (IndA) and PfkB-type carbohydrate kinase family protein (pxPfkB; Eubel et al., 2008; Reumann, 2011), IndA harbors a PTS2 (RIX_5HL), and pxPfkb has a PTS1 (SML>) in *Arabidopsis*, whereas in rice IndA contains a PTS1 (SAL>) and pxPfkb has a PTS2 (RMX_5HL). In a similar case, the *Arabidopsis* HIT2 and HIT3 proteins both have PTS2 (RLX_5HL and RVX_5HF respectively) and HIT1 has a PTS1 (SKV>), whereas in rice all three putative peroxisomal HIT proteins have PTS2s (RLX_5HL). A third example is the acquisition of a minor PTS2 (RQX_4HL) in one of the putative homologs of epoxide hydrolase (EH) in rice.

EXPANSION AND CONTRACTION OF PEROXISOMAL PROTEIN FAMILIES IN RICE

Rice is considered to be an ancient polyploid, as evidenced by remnants of duplicated blocks in its genome (Paterson et al., 2004). Its genome is predicted to have 1.5 times as many protein coding genes as those in *Arabidopsis* (Sasaki et al., 2008). Thus, many *Arabidopsis* peroxisome proteins or protein families have expanded in number in the rice genome, augmenting the number of rice peroxisome proteins.

Among the rice peroxisome proteins, PEX11a, MDAR4, polyamine oxidase (PAO), a protein of unknown function (UP3), AAE1, AAE7, and PM16 seem to have undergone tandem duplications. Duplication of genes is a recurrent evolutionary strategy that drives genetic diversity, and divergent expression of duplicated genes has shaped functional evolution of proteins and is crucial for their retention in the genome (Gu, 2003; Pal et al., 2006; Innan and Kondrashov, 2010). Consistent with this, the duplicated genes in each pair of the tandem duplicates of PAO, UP3, AAE7, and MDAR4 show highly dissimilar expressions (http://evolver.psc.riken.jp/seiken/OS/index.html).

The peroxisomal ATP-binding cassette (ABC) transporter PXA1/CTS/PED3 appears to have two homologs in rice. PXA1/CTS/PED3 has been attributed with a role in transporting β-oxidation substrates into the peroxisome, and mutant analysis in *Arabidopsis* uncovered a plethora of plant phenotypes associated with its malfunction (Zolman et al., 2001b; Hayashi et al., 2002; Theodoulou et al., 2006; Footitt et al., 2007b). In yeasts and mammals, the PXA1 function is executed by two proteins (each being a half transporter), which heterodimerize to form a functional complex (Hettema and Tabak, 2000; Wanders et al., 2007). However, the rice PXA1 homologs, like *Arabidopsis* PXA1, encode for full transporters and presumably have full activity. It will be worthwhile to explore as to whether the two rice homologs have

different substrate specificities and whether this feature is unique to monocots.

Genes encoding several enzymes associated with the major peroxisomal functions, such as β-oxidation and related functions and detoxification, also increased in numbers in rice. Examples include fatty acid multifunctional protein (MFP), acyl-CoA oxidase (ACX), small thioesterase (sT), esterase/lipase/thioesterase family 1 (ELT1), OPR3 in JA biosynthesis, and napthoate synthase (NS), which has a predicted role in benzoate or phylloquinone metabolism. It will be interesting to investigate whether the acquisition of these additional copies of genes resulted in diversification of the enzymatic activities. β-oxidation activities are the primary source of H_2O_2 generation in peroxisomes. MDAR and APX are two major enzymes in the glutathione–ascorbate cycle, which serves to eliminate toxic H_2O_2. In line with the expanded core of β-oxidation enzymes, which are capable of generating H_2O_2, the antioxidative enzyme complement, including MDAR1, APX3, and GSTT, has also undergone concomitant expansion. EHs are involved in removal of toxic metabolites and enzymatic byproducts, thus fulfilling an important role in peroxisomal detoxification. In rice, there seems to have four peroxisome EHs, in contrast to the presence of a single EH in the *Arabidopsis* peroxisome. A study in *Nicotiana* suggests that peroxisomal EH may play a role in basal resistance during fungal infection (Wijekoon et al., 2011). It will be worthwhile to analyze if they are involved in pathogen response in rice as well.

Biotin is a vitamin and an important cofactor of enzymes in both decarboxylation and carboxylation reactions; their biosynthetic enzymes have been shown to be mostly mitochondrial (Smith et al., 2007; Asensi-Fabado and Munne-Bosch, 2010). Biotin F (7-keto-8-aminopelargonic acid synthase), an enzyme implicated in the first step of biotin biosynthesis, has been a recent and surprising addition to peroxisome localized proteins in *Arabidopsis* (Tanabe et al., 2011). Biotin F has two rice homologs, both of which contain the canonical PTS1, SKL. Production of vitamins is an economically important agricultural trait that is often exploited to enhance nutritional value of food crops (Potrykus, 2001; Beyer et al., 2002; Datta et al., 2003). Investigations into the impact of these proteins on the biotin content of the crops would define new functions of peroxisomes and be vital in understanding the contributions of peroxisomes in this process.

Betaine aldehyde dehydrogenases (BADH) metabolize 4-aminobutyraldehyde/Δ1-pyrroline and probably function in polyamine catabolism in peroxisomes. Rice has two copies of this gene, and the genetic basis of fragrance in rice was linked to the BADH2 locus. Interestingly, the non-functional BADH2 allele causes fragrance production, because the accumulation of the substrate, 4-aminobutyraldehyde/Δ1-pyrroline, in this allele enhances the synthesis of 2-acetyl-1-pyrroline, a major volatile responsible for aroma in rice (Bradbury et al., 2008; Chen et al., 2008). BADH1, on the other hand, was reported to oxidize acetaldehyde and might be important to relieve oxidative stress related to the submergence and re-aeration of rice plants (Mitsuya et al., 2009).

Two peroxisome membrane proteins, PEX22 and FIS1, which serve as scaffolds to recruit downstream proteins (PEX4 and DRP3, respectively) in peroxisome biogenesis (Zolman et al., 2005; Scott et al., 2006; Lingard et al., 2008; Zhang and Hu, 2008, 2009), both seem to have an additional homolog in rice. However, subcellular targeting analysis needs to be done to verify this observation, as targeting signals for peroxisome membrane proteins are hard to define.

Conversely, some *Arabidopsis* multigene family proteins only have a single equivalent gene in rice. PEX19 and PEX3 are involved in peroxisome membrane protein import and both have two isoforms in *Arabidopsis* (Kaur et al., 2009); yet only one copy each is found in rice. The two peroxisomal adenosine nucleotide transporters PNC1 and PNC2 were suggested to have arisen from genomic chromosomal rearrangements (Palmieri et al., 2011), therefore the occurrence of a single-copy PNC in rice is not unreasonable. Lastly, citrate synthase (CSY), glutamate:glyoxylate aminotransferase (GGT), 3-ketoacyl-CoA thiolase (KAT), and acetyltransferase (ATF) have multiple isoforms in *Arabidopsis* but seem to be encoded by a single gene in rice. Mutants for these single-copy genes may be promising candidates to bypass gene redundancy problems encountered in *Arabidopsis* to unveil the function of their protein products in plants.

FUTURE PERSPECTIVES

Proteomics provide a wealth of information regarding organelle protein constituents, yet there are limitations to this approach. Many membrane proteins along with low-abundance proteins and proteins peripherally associated with peroxisomes tend to escape detection. In fact, none of the plant mass spectrometry-based proteome studies were successful in identifying most known peroxisomal membrane proteins, including those involved in various aspects of peroxisome biogenesis. However, many of their counterparts were successfully discovered in previous peroxisomal proteomics experiments in yeasts and mammals (Schafer et al., 2001; Kikuchi et al., 2004; Wiese et al., 2007). As such, there is still a lot of space for technology improvement to maximize the coverage of plant peroxisomal proteins, especially those associated with the membrane. In addition, peroxisomes and other organelles are not static entities within the cell. Some proteins may be accumulated or redistributed in the peroxisome in response to varied stimuli in a tissue-, environment-, or development-specific manner, and as a result, underrepresented in the analyzed proteome. Therefore, sampling of the peroxisome proteome at various developmental stages and under different environmental conditions may uncover proteins with provisional presence in these organelles.

Since experimental proteomics has its limitations in detecting low-abundance and transient peroxisomal proteins, this approach needs to be complemented by *in silico* protein prediction studies in order to completely decode the peroxisome proteome. Bioinformatics approaches have been very powerful in predicting peroxisomal proteins based on the presence of PTSs on them, allowing researchers to verify the predictions by subcellular localization studies (Kamada et al., 2003; Reumann et al., 2004; Lingner et al., 2011; Reumann, 2011). Furthermore, to assign functions to each newly identified peroxisomal protein, reverse genetics analysis and biochemical characterizations need to be conducted. In the *Arabidopsis* peroxisome 2010 project, we have analyzed more than 90 sequence-indexed T-DNA insertion mutants of over 50 novel peroxisomal genes through a series of physiological, biochemical, and cell biological assays to assess the roles of the corresponding proteins in peroxisomes. This systematic

approach revealed the involvement of more peroxisomal proteins in embryogenesis, peroxisome protein import, and defense response (Cassin and Hu, unpublished). Other physiological assays coupled with metabolic profiling will need to be employed to elucidate the novel roles of plant peroxisomes, as our current tool box for analyzing peroxisome-related functions is only limited to the well known peroxisomal functions such as β-oxidation and photorespiration.

Knowledge gained through organelle proteomics can help us build increasingly complex models regarding the functions and regulation of these compartments, and map metabolic fluxes in relation to other organelles. Cross comparison of global environmental stress proteomics data using known peroxisome proteins identified proteins with changed abundance under salt (6PGL, NDPK1), cadmium (MDAR1, ATMS1, CAT3), and cold (CAT3) stresses (Taylor et al., 2009). Post-translational modification (PTM) of plant peroxisomal proteins is a field that has been unexplored, except for the phosphorylation of PMP38/PXN reported by Eubel et al. (2008). The list of *Arabidopsis* peroxisomal proteins can be used to query preexisting databases that compile data of global PTM events. Information extracted from the databases can then be used to formulate hypothesis, followed by experimental testing.

A systems biology approach, which combines functional genomics, proteomics, and computational tools, may help to establish a global network of peroxisome function in plants. Studies in yeasts at the systems level defined the network dynamics that control the response of yeast cells to fatty acids at multiple levels, including signaling, transcription, chromatin dynamics, and peroxisome biogenesis (Saleem et al., 2010a,b). Three transcription factors in yeast have been demonstrated to be directly responsible for transcriptional regulation of peroxisome biogenesis genes as well as metabolic enzymes therein during response to oleic acids (Gurvitz and Rottensteiner, 2006). Likewise, the mammalian nuclear receptor, PPARα, controls the activation of peroxisomal genes in response to metabolic stimuli (Desvergne and Wahli, 1999). Plant peroxisome proteins far outnumber those found in yeasts or mammals, i.e., over 160 in *Arabidopsis* and (putatively) more than 190 in rice, vs. 61 in *Saccharomyces cerevisiae* and 85 in humans (Schrader and Fahimi, 2008). Yet how transcriptional regulation of peroxisomal genes is accomplished in plants is largely unknown. Direct binding of two transcriptional factors to promoters of peroxisome genes in plants has been reported. The first is the bZIP transcription factor, HY5 homolog (HYH), which binds to the promoter of the peroxisome proliferator gene *PEX11b* and controls its light specific activation in a phytochrome A-dependent manner, resulting in light-induced peroxisome proliferation (Desai and Hu, 2008). In addition, using chromatin immunoprecipitation-on-chip analysis, PEX11b and a glyoxalase I homolog (GLX1) were found to be direct targets of the bHLH transcription factor POPEYE (PYE) under iron deplete conditions (Long et al., 2010). We can now use the inventory of *Arabidopsis* peroxisome proteins in combination with available global expression datasets to build transcriptional regulatory networks based on co-expression analysis. Mining such data should also enable us to connect common expression patterns to possible regulatory factors. This knowledge would be instrumental to broadening our understanding of what factors govern peroxisome protein composition in plants and how they relate to global environmental or developmental changes.

Given the agronomical importance of plant peroxisomes, extending the large scale proteome study of these organelles into crop plants will be highly beneficial to improving the quality, yield, and stress response of crop species. In addition to the *in silico* proteome analysis of rice peroxisomes performed in this study, experimental proteomics should be employed to understand the dynamic rice peroxisomal proteome in different tissues and developmental stages, and under various environmental cues. Comparison of the peroxisome proteomes in rice and *Arabidopsis* will shed light onto the evolution of peroxisomal functions in diverse plant lineages. Grass (Poaceae) genomes display extensive synteny (Devos and Gale, 1997), thus information gained from rice could be applied to other cereal crops such as maize and wheat, which are also prominent food crops worldwide.

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