

Plant peroxisomes: recent discoveries in functional complexity, organelle homeostasis, and morphological dynamics

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Peroxisomes are essential for life in plants. These organelles house a variety of metabolic processes that generate and inactivate reactive oxygen species. Our knowledge of pathways and mechanisms that depend on peroxisomes and their constituent enzymes continues to grow, and in this review we highlight recent advances in understanding the identity and biological functions of peroxisomal enzymes and metabolic processes. We also review how peroxisomal matrix and membrane proteins enter the organelle from their sites of synthesis. Peroxisome homeostasis is regulated by specific degradation mechanisms, and we discuss the contributions of specialized autophagy and a peroxisomal protease to the degradation of entire peroxisomes and peroxisomal enzymes that are damaged or superfluous. Finally, we review how peroxisomes can flexibly change their morphology to facilitate inter-organellar contacts.

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Introduction

Peroxisomes are small organelles found in most eukaryotes that are delimited by a single lipid bilayer. Diverse metabolic activities are compartmentalized in plant peroxisomes (Table 1). Well-established peroxisomal activities include fatty acid β -oxidation, hormone production, and photorespiration. Peroxisomal pathways often include an oxidative step generating reactive oxygen species (ROS) as byproducts; peroxisomes therefore also house catalase and other ROS-inactivating enzymes.

Peroxisomes primarily proliferate by growth and division (Figure 1). The proteins required for peroxisome biogenesis, matrix protein import, and division are designated as peroxins (PEX proteins). Peroxisomal matrix proteins are imported into the organelle with the assistance of two interacting receptors, PEX5 for peroxisome-targeting signal type 1 (PTS1) proteins and PEX7 for PTS2 proteins (Figure 2). The cargo-loaded receptors dock at the peroxisomal membrane via interactions with PEX13 and PEX14 and release their cargo into the matrix by largely unknown mechanisms. Membrane-associated PEX5 is ubiquitinated, extracted from the membrane and retrotranslocated back to the cytosol for additional import rounds. After arrival in the matrix, the PTS2 domain is removed, whereas PTS1 proteins retain the signal (Figure 2).

Peroxisomal membrane proteins (PMPs) are inserted into peroxisomes either directly or via the ER membrane, from which pre-peroxisomes can bud and mature by post-translational import of matrix and additional membrane proteins into the organelle (Figure 1). PMPs include a subset of the PEX proteins necessary for import of matrix proteins into the organelle. Mature peroxisomes extend, tubulate, and divide by fission, which is considered to be the predominant mode of peroxisome proliferation (Figure 1).

Although key peroxins and core peroxisomal functions are largely conserved in eukaryotes, there are important differences among fungal, animal, and plant peroxisomes. These distinctions underscore the need for a thorough knowledge of peroxisome biology at all levels in the reference plant *Arabidopsis thaliana*, which is prerequisite for translation to crop plants and microalgae for future agricultural and biotechnological applications. In this article, we highlight recent discoveries that have deepened our understanding of the functional plasticity, biogenesis, degradation, and membrane dynamics of peroxisomes in plants.

Functional diversity of plant peroxisomes

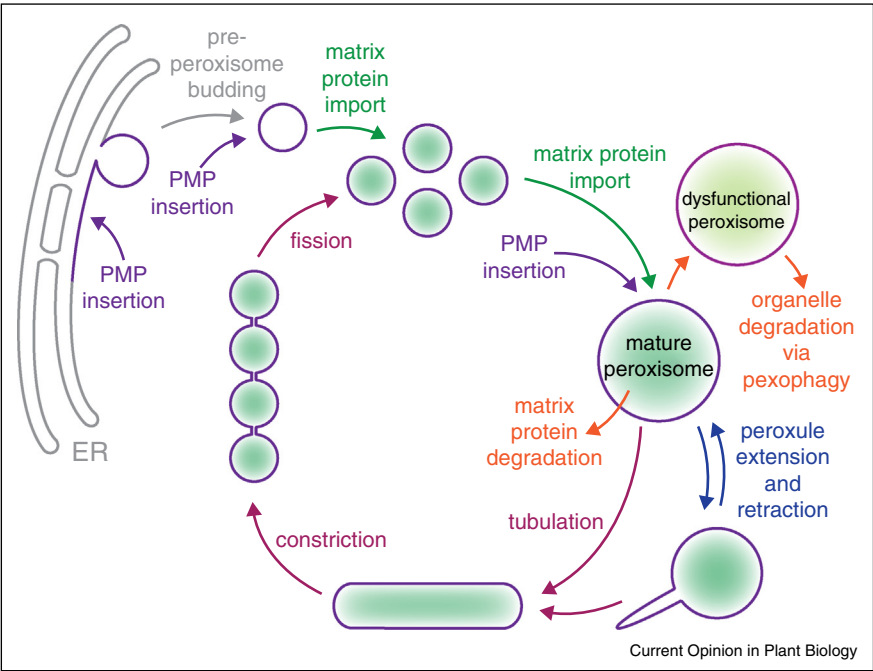
The metabolic diversity and plasticity of peroxisomes is amazing (Table 1), and unexpected functions of plant peroxisomes continue to be discovered. For instance, peroxisomes house biosynthetic steps of phylloquinone (2-methyl-3-phytyl-1,4-naphtho-quinone or vitamin K₁), a vital co-factor for electron transfer in photosystem I. Phylloquinone biosynthesis begins in plastids with the

Table 1	
Plant peroxisome functions	
Functions	Metabolites or proteins
Catabolic	
ROS detoxification	H ₂ O ₂ , O ₂ ^{•−}
Fatty acid β-oxidation	Straight-chain, branched, saturated, unsaturated fatty acids
Catabolism of primary metabolites	Purines, branched-chain amino acids
Catabolism of secondary metabolites	Polyamines
Defense compound metabolism	Indole glucosinolates
Biosynthetic	
ROS generation	H ₂ O ₂ , O ₂ ^{•−} , NO
Glyoxylate cycle	C ₄ metabolite (succinate)
Photorespiration	C ₃ metabolite and amino acids (glycerate, glycine, serine)
Hormone biosynthesis	Jasmonic acid (JA) and indole-3-acetic acid
Co-factor biosynthesis (and recycling)	Phylloquinone, biotin, NAD(P)H
Secondary metabolism	Polyamines, benzoic acid, isoprenoids (mevalonate)
Non-metabolic	
Protein processing and degradation	DEG15, LON2
Reversible phosphorylation	CPK1, GPK1, PP2A
Calcium signaling	CML3

synthesis of *o*-succinylbenzoate from chorismate. Peroxisomal enzymes catalyze the next three steps to the double-ring structure of naphthoquinone: (i) activation via CoA esterification by acyl-activating enzyme 14, (ii) ring cyclization by naphthoate synthase to yield the CoA thioester of 1,4-dihydroxy-2-naphthoate (DHNA) [1], and (iii) hydrolysis of DHNA-CoA by two functionally redundant peroxisomal thioesterases [2]. Phylloquinone biosynthesis is finalized in chloroplasts by DHNA prenylation and methylation. Interestingly, while most phylloquinone biosynthetic enzymes are of cyanobacterial origin, the thioesterases apparently originate from Lactobacillales by horizontal gene transfer [2]. Because none of the three peroxisomal enzymes of phylloquinone biosynthesis produces ROS, it remains to be elucidated why these steps were shifted from chloroplasts to peroxisomes during higher plant evolution.

The first enzyme in biotin synthesis (BioF) is peroxisomal in plants and fungi [3,4], while the subsequent steps are mitochondrial. Moreover, peroxisomal β-oxidation is required for synthesis of the BioF substrate, pimeloyl-CoA [3,4]. In addition, the enzymes catalyzing the final two steps of mevalonate biosynthesis, 5-phosphomevalonate kinase and mevalonate 5-diphosphate decarboxylase, were recently characterized as peroxisomal in *Arabidopsis* and *Catharanthus roseus* [5].

Figure 1



Peroxisome dynamics. Peroxisomal membrane proteins (PMPs) are inserted directly into peroxisomes or into the ER membrane from which pre-peroxisomes can bud. PMPs include a subset of the PEX proteins necessary for import of matrix proteins into the organelle (Figure 2). Mature peroxisomes extend and retract peroxules, tubulate, and divide by fission, which is considered to be the predominant mode of peroxisome proliferation. Peroxisomal quality control includes degrading damaged or obsolete matrix proteins and eliminating dysfunctional or superfluous peroxisomes via pexophagy, a specialized form of autophagy.

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