Available online at www.sciencedirect.com
ScienceDirect
Biochimica et Biophysica Acta 1763 (2006) 1382–1391
BIOCHIMICA ET BIOPHYSICA ACTA
BBA
www.elsevier.com/locate/bbamcr

Review

Arabidopsis thaliana—A model organism to study plant peroxisomes

Makoto Hayashi, Mikio Nishimura *

National Institute for Basic Biology, Okazaki 444-8585, Japan

Received 7 June 2006; received in revised form 28 July 2006; accepted 18 August 2006
Available online 22 August 2006

Abstract

In higher plants, peroxisomes have been believed to play a pivotal role in three metabolic pathways, which are lipid breakdown, photorespiration and H_2O_2-detoxificaton. Recently, significant progress in the study of plant peroxisomes was established by forward-/reverse-genetics and post-genomic approaches using *Arabidopsis thaliana*, the first higher plant to have its entire genome sequenced. These studies illustrated that plant peroxisomes have more diverse functions than we previously thought. Research using *Arabidopsis thaliana* is improving our understanding of the function of plant peroxisomes.

Keywords: Arabidopsis; Glyoxysome; Leaf peroxisome; Lipid metabolism; Photorespiration

1. Introduction

From the mid 1980s, *Arabidopsis thaliana* (referred to herein as Arabidopsis) became an essential model plant for plant scientists due to the availability of various information and tools, such as whole genome sequence, molecular genetic markers and large collections of sequence-indexed DNA-insertion mutants, in addition to the ease of generating transgenic plants. This is also the case for scientists engaged in studying plant peroxisomes. In this review, we briefly summarize the unique features of plant peroxisomes, and then describe the recent progress achieved by introducing Arabidopsis as tools for forward-/reverse-genetics and post-genome approaches.

2. Unique features of plant peroxisomes

Almost four decades have passed since the first discovery of plant peroxisomes. Much of our present knowledge of plant peroxisomes was established in the first era of research using biochemical and morphological techniques [1–3]. These studies clearly showed that peroxisomes in higher plants have distinct features compared to other organisms, although they also share some common features such as detoxification of H_2O_2 by catalase. One of the remarkable features of peroxisomes in higher plants is the plasticity of their functions. Plant peroxisomes are known to differentiate in function depending on the cell type. Therefore, they are subdivided into three different classes, namely glyoxysomes, leaf peroxisomes and unspecialized peroxisomes. Additionally, in some plant species ureide metabolism takes place in peroxisomes.

Glyoxysomes are present in cells of storage organs, such as endosperms and cotyledons, during post-germinative growth of oil-seed plants, as well as in cells of senescent organs [2,4]. They play an important role in lipid metabolism (Fig. 1). In dry seeds, large amounts of triacylglycerols accumulate as reserved lipids in organelles called oil bodies. Triacylglycerols in oil bodies mainly contain long-chain fatty acids such as palmitic acid (C16:0), stearic acid (C18:0), oleic acid (C18:1), linoleic acid (C18:2) and linolenic acid (C18:3) [5]. During the post-germinative growth of the seedlings, fatty acids released from the triacylglycerols are metabolized to produce sucrose. Sucrose provides a carbon source that is necessary for growth before the plants begin photosynthesis. The conversion of fatty acids to succinate takes place in the glyoxysomes via fatty acid β-oxidation and the glyoxylate cycle (Fig. 1). It is worth noting that the glyoxysome is the sole (or at least predominant) site of fatty acid β-oxidation in plants, and completely degrades fatty acids into acetyl CoA by the action of acyl CoA oxidases with various substrate specificities involving short-chain specific acyl

* Corresponding author. Tel.: +81 564 55 7500; fax: +81 564 55 7505.
E-mail address: mikosome@nibb.ac.jp (M. Nishimura).

0167-4889/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbamcr.2006.08.014

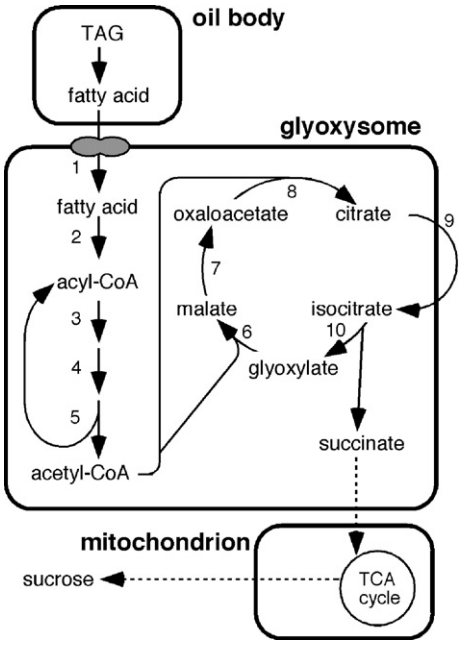

Fig. 1. Gluconeogenesis from seed reserved lipids (TAG; triacylglycerol) during germination. Within the entire gluconeogenic pathway, the conversion of fatty acids to succinate takes place in the glyoxysomes via fatty acid β-oxidation (1–5) and the glyoxylate cycle (6–10). The enzymes involved in these pathways are: 1, full size ABC transporter; 2, acyl-CoA synthetase; 3, long-, medium- and short-chain acyl-CoA oxidases; 4, the multifunctional protein possessing enoyl-CoA hydratase and 3-hydroxyacyl-CoA dehydrogenase activities; 5, 3-ketoacyl-CoA thiolase; 6, malate synthase; 7, malate dehydrogenase; 8, citrate synthase; 9, aconitase; 10, isocitrate lyase. Aconitase is the only enzyme for glyoxylate cycle that is not localized in the glyoxysome.

CoA oxidase. [6–8]. Fatty acid β-oxidation and glyoxylate cycle are discussed in detail elsewhere in this volume.

Leaf peroxisomes are widely found in cells of photosynthetic organs, such as green cotyledons and leaves [9]. In C3 plants, these organs have a light-dependent O_2 uptake and CO_2 release called photorespiration. This physiological phenomenon is initiated by the oxygenase reaction of ribulose bisphosphate carboxylase/oxygenase (RuBisCO; a key enzyme for CO_2 fixation in photosynthesis) that depends on the O_2 concentration and light intensity. Two phosphoglycolates, byproducts of the oxygenase reaction, are converted to produce one phosphoglycerate, an intermediate of the Calvin–Benson cycle, and one CO_2 by the photorespiratory glycolate pathway. This pathway involves many enzymatic reactions located in leaf peroxisomes, chloroplasts and mitochondria. Within the entire photorespiratory glycolate pathway, leaf peroxisomes possess glycolate oxidase, hydroxypyruvate reductase and some aminotransferases (Fig. 2). By the combination of these enzymes, leaf peroxisomes convert glycolate to glycine and serine to glycerate. Photorespiration is also discussed in detail elsewhere in this volume.

Glyoxysomes, leaf peroxisomes and unspecialized peroxisomes are known to interconvert in their functions between each other during certain cellular processes. The functional transformation of plant peroxisomes has been most extensively studied using oil seed plants. For example, reversible interconversion between glyoxysomes and leaf peroxisomes is observed during greening and senescence of the cotyledonary cells [10–14]. When the seeds germinate, seedlings start to grow using the seed reserve substances in etiolated cotyledons. After the seedlings grow and are then irradiated, the etiolated cotyledons become green and produce energy by photosynthesis. To support the drastic metabolic change, glyoxysomes are directly transformed into leaf peroxisomes during the greening process of the cotyledons. Once seedlings expand their leaves, green cotyledons gradually undergo senescence. With the process of senescence, reverse transformation from leaf peroxisomes to glyoxysomes occurs in the cotyledonary cells. Induction of glyoxysomes from leaf peroxisomes is also found in cells of other senescent organs, such as leaves and petals.

It was fortunate that defects in glyoxysomal and leaf peroxisomal function in Arabidopsis mutants could be easily visualized (Fig. 3, see in detail below). Due to this reason, Arabidopsis became the most frequently used plant for studying plant peroxisomes. Forward-/reverse-genetics and post-genome approaches using Arabidopsis are opening up a second era of research for plant peroxisomes.

3. Forward genetic analyses

One of the significant contributions of Arabidopsis is the isolation and characterization of peroxisome-defective mutants by forward genetics. In 1980, *sat*, the first plant mutant with a defect in peroxisomal function, was identified from a collection of mutants with defects in the photorespiratory glycolate pathway [15]. The screening procedure for the collection was based on the observation that plants still show normal or even enhanced growth in an atmosphere containing a relatively high CO_2/O_2 ratio that inhibits photorespiration. The expectation was that mutant plants with reduced photorespiration would show conditional defects in growth depending on the CO_2

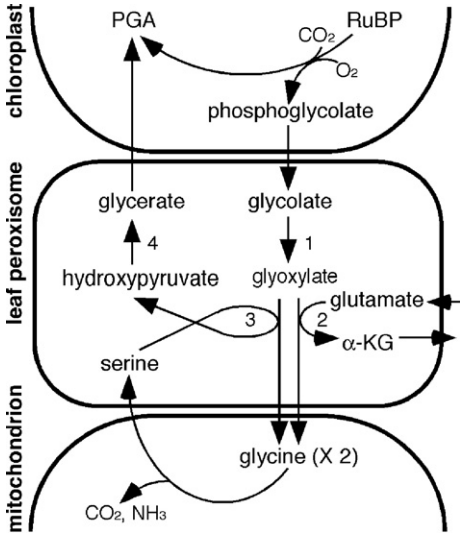

Fig. 2. Photorespiratory glycolate metabolism in photosynthetic tissue of C3 plants. Within the entire photorespiratory glycolate pathway, leaf peroxisome converts glycolate to glycine and serine to glycerate. The enzymes involved in this metabolism are: 1, glycolate oxidase; 2, glutamate-glyoxylate aminotransferase; 3, serine-glyoxylate aminotransferase; 4, hydroxypyruvate reductase.