



## Review

An engineered plant peroxisome and its application in biotechnology<sup>☆</sup>

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## ABSTRACT

Plant metabolic engineering is a promising tool for biotechnological applications. Major goals include enhancing plant fitness for an increased product yield and improving or introducing novel pathways to synthesize industrially relevant products. Plant peroxisomes are favorable targets for metabolic engineering, because they are involved in diverse functions, including primary and secondary metabolism, development, abiotic stress response, and pathogen defense. This review discusses targets for manipulating endogenous peroxisomal pathways, such as fatty acid  $\beta$ -oxidation, or introducing novel pathways, such as the synthesis of biodegradable polymers. Furthermore, strategies to bypass peroxisomal pathways for improved energy efficiency and detoxification of environmental pollutants are discussed. In sum, we highlight the biotechnological potential of plant peroxisomes and indicate future perspectives to exploit peroxisomes as biofactories.

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## Contents

1. Introduction	232
2. Improving seed oil yield and quality	233
3. Plant peroxisomes confer stress tolerance	233
3.1. Increasing the peroxisome population	233
3.2. Improving peroxisomal ROS-scavenging systems	234
3.3. Improved pest and pathogen resistance	235
3.4. Peroxisomal small heat shock proteins for enhanced stress tolerance	235
4. Modulating auxin synthesis in peroxisomes	235
5. Implementation of artificial metabolic pathways to gain novel peroxisomal functions	235
5.1. Production of biodegradable polymers in plant peroxisomes	235
5.2. Peroxisomal bypass pathways to reduce photorespiration	236
5.3. Peroxisomal degradation pathways for pollutants	236
6. Concluding remarks	237
Acknowledgements	238
References	238

**Abbreviations:** H<sub>2</sub>O<sub>2</sub>, hydrogen peroxide; JA, jasmonic acid; PHA, polyhydroxyalkanoate; ROS, reactive oxygen species.

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## 1. Introduction

Plants have evolved the ability to produce a wide range of molecules. Many of these compounds are of biotechnological importance, as they serve as food, colorants, flavors, fragrances, traditional medicines, pharmaceuticals, cosmetics, and renewable fuels [1]. Their chemical synthesis is often difficult and expensive, thus genetic engineering is an alternative approach to optimize the production of desired metabolites in plants.

In plants, biochemical pathways are compartmentalized and individual steps of a particular pathway are distributed over

different compartments. In this context, peroxisomes, which are subcellular organelles 1  $\mu\text{m}$  in diameter [2], represent as organelles at a metabolic crossroads [3,4], because they participate in one or more steps in many significant metabolic reactions, including primary carbon metabolism (e.g. beta-oxidation of fatty acids and photorespiration), secondary metabolism (e.g. production of glucosinolates), development (e.g. synthesis of plant hormones), abiotic stress response, and pathogen defense [4].

Thus, peroxisomes are an attractive target for metabolic engineering, to increase yield and quality of plant products. Manipulation of peroxisomal scavenging systems for reactive oxygen species (ROS) might enhance plant fitness under environmental stress conditions [5]. Besides altering peroxisomal functions, novel pathways can be implemented in peroxisomes, enabling the synthesis of desired metabolites or degradation of toxic molecules. The following characteristics illustrate why peroxisomes are well suited for biotechnological purposes:

- (i) Peroxisomes are surrounded by a single lipid bilayer membrane [4]. Novel reactions can be compartmentalized within peroxisomes. A peroxisomal compartmentation is favorable because end products or intermediates can be toxic for the cell. As peroxisomes are equipped with efficient ROS-detoxifying systems [6], ROS-producing reactions can be introduced in peroxisomes without deleterious effects.
- (ii) Peroxisomes allow an efficient targeting of heterologous proteins, since protein-targeting signals for the peroxisome are well established. Soluble, nuclear-encoded proteins are targeted to peroxisomes by two different targeting signals, which direct soluble proteins to peroxisomes. Most proteins use the Type 1 Peroxisomal Targeting Signal (PTS1) to enter peroxisomes, which consists of three amino acids at the carboxyl terminus (SKL, or a conserved variant) [7,8]. The Type 2 Peroxisomal Targeting Signal (PTS2) is a conserved nonapeptide (9 amino acids), which is attached to the amino terminus of peroxisomal proteins [9]. Fusion of either signal peptide to a heterologous protein results in direct targeting to peroxisomes. Thus, the enzymatic content of peroxisomes can be easily modified. In contrast to plastids and mitochondria, the peroxisomal protein import machinery is able to import fully folded proteins and stable protein complexes in a receptor-independent fashion [4]. The import of heterologous protein complexes into peroxisomes depends on a mechanism called piggybacking, where a protein without a peroxisomal targeting signal uses a PTS-carrying protein as shuttle [10,11]. Therefore, coupling of a shuttle protein to other proteins might enable the targeting of even larger protein complexes to peroxisomes without modifying the import receptor machinery.
- (iii) Peroxisomes are highly dynamic organelles, which are able to adjust size and number [12]. They multiply by fission and proliferation [4]. Latter is induced by various environmental, developmental and metabolic cues and is controlled by the PEROXIN11 protein family and several transcription factors [13,14]. A rapid increase in peroxisome number allows an accumulation of substances produced in peroxisomes [2].

In recent years, major progress has been made in genomics and proteomics, revealing the diversity of peroxisomal metabolism [4,15]. However, mechanisms to exploit plant peroxisomes for optimizing metabolism or modifying metabolic fluxes toward compounds of interest are not well studied. Here, we present recent pioneering approaches to produce plant peroxisome biofactories. Moreover, we indicate putative targets and possible strategies that in the future could be exploited to engineer peroxisomes for biotechnological purposes.

## 2. Improving seed oil yield and quality

One of the major goals of agricultural biotechnology is to increase the content and/or improve the value of oils in oilseed plants, including sunflower, soybean, palm, oilseed rape, and maize crops [16]. Oilseed crops are not only important for human nutrition [17], but can also be used for a variety of chemical applications.

Plants are able to produce a wide range of different fatty acids, whereas the number of fatty acids shared between plant species is relatively low. All conventional crops contain palmitic acid, stearic acid, oleic acid, linoleic acid, and linolenic acid. These are termed “usual” fatty acids. Fatty acids, which in their chemical structures differ from usual fatty acids, are referred to as “unusual” fatty acids. Unusual fatty acids, exhibiting hydroxylations or acetylations, are of major industrial interest, as they provide raw materials for the generation of biopolymers or fuels [18].

Vegetable oils, for example, serve as a sustainable replacement of petroleum-based chemicals [16]. One appealing method to produce high-value oils is the genetic engineering of plants accumulating ricinoleic acid, which serves as precursor for economically-viable products, such as ink, lubricants, varnishes, emulsifiers, nylon, or biodiesel [18,19].

The bottleneck for increased oilseed content and the production of ‘designer oils’ is the channeling of fatty acids into storage oil. Inefficient integration arises either by enhanced biosynthesis of native fatty acids or by the low affinity of acyltransferases to unusual fatty acids [20,21]. As a consequence, accumulated fatty acids are degraded via peroxisomal beta-oxidation, which simultaneously operates during lipid synthesis (Fig. 1).

Inactivating peroxisomal beta-oxidation enzymes by using specific promoters only active during seed filling could minimize such futile cycling. Another strategy is to produce the desired oil in a specific plant tissue with low beta-oxidation activity (e.g. leaves). Leaf-specific oil production might be favorable if the accumulation of industrial-valuable oil in seeds affected germination or seedling establishment [22].

## 3. Plant peroxisomes confer stress tolerance

Various abiotic and biotic stress conditions, such as salinity, heat, cold, drought, and pathogen infection induce oxidative stress in plants. This results in overproduction of ROS in chloroplasts, mitochondria, and peroxisomes, with highly oxidative metabolism [23,24]. Plants are unable to escape exposure to environmental stresses, thus they have developed a complex antioxidant defense system to control ROS levels and protect cells from oxidative injury [6]. Here, we present several strategies to improve stress tolerance in plants through modified peroxisomal metabolism circumventing oxidative stress and thereby increasing fitness [25].

### 3.1. Increasing the peroxisome population

Plant peroxisomes multiply under stress conditions. In plants the PEROXIN11 family, which consist of five isoforms (a–e), controls proliferation of peroxisomes. When overexpressed, the number of peroxisomes increases. Conversely, reducing the expression of PEX11 genes results in decreased peroxisome abundance [26]. The expression of PEX11b is controlled through a phytochrome A-dependent pathway, involving the far-red light photoreceptor phyA and the bZIP transcription factor HY5 homolog [13,27].

Additionally, peroxisomal proliferation is induced by environmental stimuli and various stresses, such as high light intensities,  $\text{H}_2\text{O}_2$ , ozone, xenobiotics, cadmium, salt, pathogens, and senescence. However, little is known about the principal molecular mechanisms [28–33]. Stress-induced peroxisome proliferation

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