



Review

Plant fatty acyl reductases: Enzymes generating fatty alcohols for protective layers with potential for industrial applications

Owen Rowland^{a,*}, Frédéric Domergue^{b,c,**}^a Department of Biology and Institute of Biochemistry, Carleton University, Ottawa, Ontario, K1S 5B6, Canada^b Université de Bordeaux, Laboratoire de Biogenèse Membranaire, UMR 5200, F-33000, Bordeaux, France^c CNRS, Laboratoire de Biogenèse Membranaire, UMR 5200, F-33000, Bordeaux, France

ARTICLE INFO

Article history:

Received 24 February 2012

Received in revised form 9 May 2012

Accepted 9 May 2012

Available online 16 May 2012

Keywords:

Fatty acyl reductase

Fatty alcohol

Wax ester

Alkyl hydroxycinnamate

Cuticle

Suberin

Sporopollenin

ABSTRACT

Primary fatty alcohols are found throughout the biological world, either in free form or in a combined state. They are common components of plant surface lipids (i.e. cutin, suberin, sporopollenin, and associated waxes) and their absence can significantly perturb these essential barriers. Fatty alcohols and/or derived compounds are also likely to have direct functions in plant biotic and abiotic interactions. An evolutionarily related set of alcohol-forming fatty acyl reductases (FARs) is present in all kingdoms of life. Plant microsomal and plastid-associated FAR enzymes have been characterized, acting on acyl-coenzymeA (acyl-CoA) or acyl-acyl carrier protein (acyl-ACP) substrates, respectively. FARs have distinct substrate specificities both with regard to chain length and chain saturation. Fatty alcohols and wax esters, which are a combination of fatty alcohol and fatty acid, have a variety of commercial applications. The expression of FARs with desired specificities in transgenic microbes or oilseed crops would provide a novel means of obtaining these valuable compounds. In the present review, we report on recent progress in characterizing plant FAR enzymes and in understanding the biological roles of primary fatty alcohols, as well as describe the biotechnological production and industrial uses of fatty alcohols.

© 2012 Elsevier Ireland Ltd. All rights reserved.

Contents

1. Introduction.....	29
2. Plant fatty acyl reductase (FAR) enzymes.....	29
2.1. FAR protein structure.....	29
2.2. Biochemical characterization of FAR enzymes.....	30
2.3. Substrate specificities of plant FARs.....	31
3. Occurrence, synthesis and function of fatty alcohols <i>in planta</i>	32
3.1. Fatty alcohols as energy storage.....	32
3.2. Fatty alcohols in cuticular waxes.....	32
3.3. Fatty alcohols in aliphatic lipid polyesters: suberin and cutin.....	33
3.4. Fatty alcohols in suberin-associated alkyl hydroxycinnamates.....	33
3.5. Fatty alcohols in pollen exine.....	34
4. Industrial applications.....	34
4.1. Natural sources of fatty alcohols and wax esters.....	35
4.2. Biotechnological production of fatty alcohols in microbes.....	35
4.3. Biotechnological production of wax esters in oilseed crops.....	36
5. Concluding remarks.....	36
Acknowledgements.....	36
References.....	36

Abbreviations: FAR, fatty acyl reductase; CoA, CoenzymeA; ACP, acyl carrier protein.

* Corresponding author. Tel.: +1 613 520 2600x4213; fax: +1 613 520 3539.

** Corresponding author at: Université de Bordeaux, Laboratoire de Biogenèse Membranaire, UMR 5200, F-33000, Bordeaux, France. Tel.: +33 0 5 57 57 15 83; fax: +33 0 5 56 51 83 61.

E-mail addresses: Owen.Rowland@carleton.ca (O. Rowland), frederic.domergue@u-bordeaux2.fr (F. Domergue).

1. Introduction

Alcohol-forming fatty acyl reductases (FARs) produce fatty alcohols that have a single hydroxyl group at the terminal position (Fig. 1). Plant primary fatty alcohols occur either in free form or are linked by an ester-bond with a fatty acid (e.g. palmitic acid) to give a wax ester or an aromatic compound (e.g. ferulic acid) to give an alkyl hydroxycinnamate (Fig. 1). These various compounds are often components of plant extracellular lipid barriers: *cuticle* coating the aerial surfaces, *suberin* found in the cell walls of various internal and external tissue layers, and *sporopollenin* found in the outer walls (exine) of pollen grains [1–4]. These barriers consist of polymerized lipids and phenolics, along with associated non-covalently linked waxes. These waxes are usually complex mixtures of very-long-chain (C20–C34) fatty acids and derivatives including primary fatty alcohols and wax esters. Wax esters can also serve as energy storage, such as in the case of jojoba (*Simmondsia chinensis*) seed oil [5].

Pioneering work using cell-free homogenates from developing jojoba cotyledons demonstrated that the synthesis of fatty alcohols from fatty acyl-CoAs is NADPH dependent [6]. This led to the purification of the jojoba FAR and the subsequent cloning of its corresponding cDNA [7]. Related proteins have subsequently been cloned and characterized from other plants, including *Arabidopsis thaliana* [4,8–11], rice [12] and wheat [13], as well as insects [14–17], mammals [18], birds [19], a phytoflagellate protist [20], a planktonic crustacean [21], and a distantly related FAR from a prokaryote, *Marinobacter aquaeolei* [22,23].

In this review, we focus on plant FARs and discuss the latest data obtained through reverse genetic studies, especially in the model plant *A. thaliana*. The occurrence, synthesis and putative roles played by fatty alcohols in plants, as well as the potential of FAR proteins for biotechnological applications are discussed.

2. Plant fatty acyl reductase (FAR) enzymes

Two general types of plant FARs have been described, distinguished according to their subcellular localization and acyl-linkage substrate specificity. The first type are microsomal enzymes acting on acyl-CoA substrates, exemplified by the seed-expressed jojoba FAR [7] and the cuticle-associated *Arabidopsis* ECERIFERUM4 (CER4)/FAR3 enzyme [8]. FARs of the second type have only recently been characterized and are plastid-localized proteins that use acyl-ACPs as substrates [4,11,12]. While the first FAR type is responsible for the synthesis of fatty alcohols in seed-storage wax esters, cuticle and suberin, the function of the second type remains elusive although data point to at least a subset involved in sporopollenin biosynthesis (see Section 3).

2.1. FAR protein structure

Active plant FAR enzymes are about 500 amino acids in length, with the plastidial isoforms containing an *N*-terminal extension containing a plastid (chloroplast) transit peptide [4,8,10–12]. Plant FARs share at least 25% identity (45% similarity) at the amino acid level excluding the *N*-terminal extensions. According to the protein structure prediction software Conserved Domains Database (CDD) [24], they all share a NAD(P)H-binding Rossmann-fold domain as well as a fatty acyl-CoA reductase ('FAR.C') domain (Fig. 2A). FARs are thus predicted to be extended short-chain dehydrogenase/reductase proteins with an α/β folding pattern and a central β -sheet at the *N*-terminus (Rossmann fold) and a fatty acyl-CoA reductase domain at the C-terminus. All plant FARs contain the motif GXXGXX(G/A) at their *N*-terminus (Fig. 2A), which resembles the canonical ADP binding domain and is probably involved in binding of NAD(P)H [25]. The FARs also contain the classic YXXXK active site motif of the short-chain dehydrogenase/reductase superfamily and fall into the SDR117E family (Fig. 2A) [26,27]. The FAR.C (or fatty acyl-CoA reductase) domain is often annotated in databases

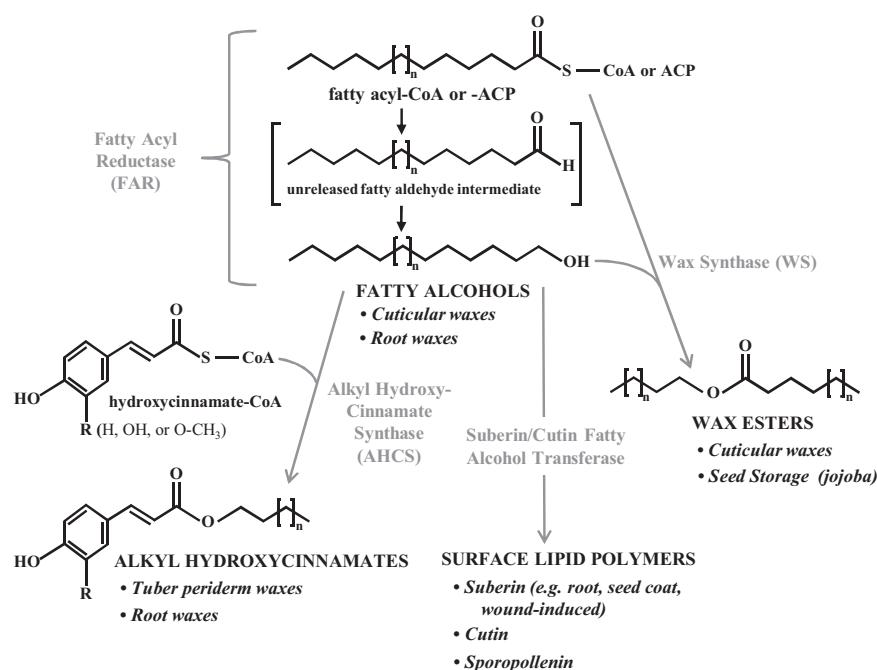


Fig. 1. Biosynthesis of fatty alcohols and derivatives. Enzyme activities are shown in grey. Free fatty alcohols are generated by fatty acyl reductases (FARs) using fatty acyl-CoA or fatty acyl-ACP as substrates (chain length ranges from C16–C30 in plants). Fatty alcohols can then be linked with fatty acids or hydroxycinnamic acids to yield wax esters and alkyl hydroxycinnamates, respectively. Fatty alcohols can also be incorporated into surface lipid polymers (suberin, cutin, and likely sporopollenin). The final major products are in uppercase and the locations where these compounds accumulate in plants are in italics.

Download English Version:

<https://daneshyari.com/en/article/2017285>

Download Persian Version:

<https://daneshyari.com/article/2017285>

[Daneshyari.com](https://daneshyari.com)