Plant Science 177 (2009) 143–155

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

Metabolism and roles of stilbenes in plants

Julie Chong [a], Anne Poutaraud [b], Philippe Hugueney [c,*]

[a] *Laboratoire Vigne, Biotechnologies et Environnement (LVBE, EA3991), Université de Haute Alsace, 33 rue de Herrlisheim, 68000 Colmar, France*
[b] *Laboratoire de Génétique et d'Amélioration de la Vigne, UMR1131, INRA, Université de Strasbourg, 28 rue de Herrlisheim, F-68021 Colmar, France*
[c] *Laboratoire Métabolisme Secondaire de la Vigne, UMR1131, INRA, Université de Strasbourg, 28 rue de Herrlisheim, F-68021 Colmar, France*

ARTICLE INFO

Article history:
Received 20 February 2009
Received in revised form 18 May 2009
Accepted 19 May 2009
Available online 27 May 2009

Keywords:
Stilbene
Resveratrol
Stilbene synthase
Defense response
Resistance

ABSTRACT

Stilbenes are a small family of plant secondary metabolites derived from the phenylpropanoid pathway, and produced in a number of unrelated plant species. These compounds have numerous implications in plant disease resistance and human health. This review first presents the stilbene biosynthesis pathway and recent advances in the characterization of stilbene biosynthetic genes in different plant species. A large body of evidence indicates that stilbenes participate in both constitutive and inducible defense mechanisms in plants, however, the detailed functions of these compounds have not been fully elucidated. The second part of this review discusses known functions of stilbenes in plants, especially in plant–pathogen and plant–herbivore relationships, or in plants subjected to abiotic stresses.

Contents

1. Introduction

Plants elaborate a vast array of natural products, which have evolved confering selective advantage against environmental stresses. Among them, the phenylpropanoids are a large family of secondary metabolites involved in plant responses to various

* Corresponding author. Tel.: +33 3 89 22 49 74; fax: +33 3 89 22 49 33.
E-mail address: philippe.hugueney@colmar.inra.fr (P. Hugueney).

0168-9452/$ – see front matter
doi:10.1016/j.plantsci.2009.05.012

stilbene	occurence	R3	R5	R3'	R4'
trans-resveratrol	*Vitis, Arachis, Fallopia*	OH	OH	H	OH
trans-piceid	*Vitis*	OGlu	OH	H	OH
pinosylvin	*Pinus,*	OH	OH	H	
piceatannol	*Picea*	OH	OH	OH	OH
pinosylvin monomethylether	*Pinus, Alnus*	OCH_3	OH	H	OH
trans-pterostilbene	*Vitis, Vaccinium*	OCH_3	OCH_3	H	OH
astringin	*Picea*	OGlu	OH	OH	OH
rhapontin	*Rheum*	OGlu	OH	OH	OCH_3

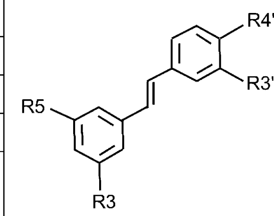

Fig. 1. Stucture of common plant stilbenes. Examples of plant genus where these stilbenes are known to occur are mentioned. OGlu: *O*-β-D-glucopyranoside.

biotic and abiotic stresses. Many phenylpropanoids are antimicrobial compounds synthesized in response to pathogen or herbivore attack and classified as phytoalexins. However, other roles have been described for stress-induced phenylpropanoids, such as signalling of defense responses, protection against UV light damage, and increase in bioavailability of recalcitrant nutrients [1]. Stilbenes are a small group of phenylpropanoids characterized by a 1,2-diphenylethylene backbone. Most plant stilbenes are derivatives of the basic unit *trans*-resveratrol (3,5,4′-trihydroxy-*trans*-stilbene) (Fig. 1), although other structures are found in particular plant families. This review does not present the diversity of stilbene structures, nor list plant taxa that contain stilbenes, as these aspects have been described elsewhere [2]. Examples of common plant stilbenes isolated from diverse plant families, including grape (Vitaceae), pine (Pinaceae), peanut (Fabaceae) and sorghum (Poaceae) are given in Fig. 1. Over the last 15 years, plant stilbenes have received considerable interest, due to their biological activities and possible pharmacological applications. Since resveratrol was postulated to be involved in the health benefits associated with a moderate consumption of red wine [3], it is one of the most extensively studied natural products. Hundreds of studies have reported that resveratrol can prevent or slow the progression of a wide variety of illnesses, including cancer, and cardiovascular diseases, as well as extend the lifespans of various organisms [4]. This review does not describe the wide ranging pharmacological applications and clinical potential of resveratrol and other stilbenes, as these subjects have been recently reviewed [4,5]. Instead, we focus on recent advances in the characterization of genes and enzymes involved in stilbene biosynthesis. Among plant stilbenes, compounds with known functions in plants are emphasized, especially in plant–pathogen and plant–herbivore relationships, or in plants subjected to abiotic stresses. Finally, the specific role of these compounds in plant resistance to pathogenic fungi is discussed.

2. Stilbene biosynthesis

Plant stilbenes are derived from the general phenylpropanoid pathway (Fig. 2). All higher plants seem to be able to synthesize malonyl-CoA and CoA-esters of cinnammic acid derivatives, but only few plant species are able to produce stilbenes. The first enzymes of the phenylpropanoid pathway will not be described in details, as phenylalanine ammonia lyase (PAL), cinnamate-4-hydroxylase (C4H) and 4-coumarate: CoA ligase (4CL) have been reviewed elsewhere [6–8]. This review focuses on enzymes catalyzing later steps of stilbene biosynthesis and modification, starting with stilbene synthase. Indeed, stilbene synthase, the pivotal enzyme of this pathway, evolved in a limited number of plant species, which thus acquired the capacity to produce stilbenes. Stilbenes may then undergo different types of modifications that are discussed below.

2.1. Stilbene synthase

Stilbene synthase (STS) is characteristic of stilbene-producing plants and catalyzes, in a single reaction, the biosynthesis of the stilbene backbone from three malonyl-CoA and one CoA-ester of a cinnamic acid derivative (most frequently cinnamoyl-CoA or *p*-coumaroyl-CoA, Fig. 2). STS protein was first purified from stressed cell suspension cultures of peanut (*Arachis hypogaea*) [9]. Cloning of two peanut *STS* genes revealed extensive homology to peanut chalcone synthase (*CHS*) gene throughout the coding region, the position of the single intron was conserved in both genes [10]. *STS* genes and cDNAs were subsequently cloned from grape (*Vitis vinifera*) [11] and scots pine (*Pinus sylvestris*) [12]. *STS* genes exist as a family of related genes in many plant species. This is the case in peanut [10], grapevine [11,13], scots pine [14] and Japanese red pine (*Pinus densiflora*) [15]. Until very recently, grapevine was the only stilbene-producing plant whose genome had been sequenced. Early Southern blot experiments suggested that the grapevine genome contains more than 20 *STS* genes [16]. Analyses of the first drafts of the grapevine genome sequence confirmed the large size of this multigene family, with an estimated number of 20–40 *STS* genes [17,18]. At least 20 different *STS* genes are expressed in grape following infection with *Plasmopara viticola*, which is consistent with this estimation [19]. It is noteworthy that the phenylalanine ammonia-lyase (*PAL*) gene family, coding for the first enzyme of the phenylpropanoid pathway, has expanded in parallel to the *STS* gene family in *Vitis*. Indeed, the *PAL* family has 13 genes in grapevine, whereas it contains only 4–8 genes in *Arabidopsis thaliana*, rice and poplar [18]. The functional characterization of a *CHS*-like gene from *Sorghum bicolor* identified the corresponding protein as a stilbene synthase [20]. This gene, named *SbSTS1*, is the only *STS* identified in a monocotyledonous plant to date. Although *STS* genes are often organized in families, sorghum is an exception to this rule, as Southern blot experiments indicated that *SbSTS1* was the only *STS* gene in this plant species [20]. This observation was recently confirmed by the sequencing of sorghum genome [21].