ELSEVIER

Available online at www.sciencedirect.com

SciVerse ScienceDirect

Current Opinion in Plant Biology

Plant sphingolipids: function follows form

Jonathan E Markham[1], Daniel V Lynch[2], Johnathan A Napier[3], Teresa M Dunn[4] and Edgar B Cahoon[1]

Plant sphingolipids are structurally diverse molecules that are important as membrane components and bioactive molecules. An appreciation of the relationship between structural diversity and functional significance of plant sphingolipids is emerging through characterization of Arabidopsis mutants coupled with advanced analytical methods. It is increasingly apparent that modifications such as hydroxylation and desaturation of the sphingolipid nonpolar long-chain bases and fatty acids influence their metabolic routing to particular complex sphingolipid classes and their functions in signaling pathways and other cellular processes, such as membrane protein targeting. Here, we review recent reports investigating some of the more prevalent sphingolipid structural modifications and their functional importance in plants.

Addresses
[1] Center for Plant Science Innovation and Department of Biochemistry, University of Nebraska-Lincoln, Beadle Center, 1901 Vine Street, Lincoln, NE 68588, USA
[2] Department of Biology, Williams College, Williamstown, MA 01267, USA
[3] Department of Biological Chemistry, Rothamsted Research, Harpenden, Herts, AL5 2JQ, UK
[4] Department of Biochemistry, Uniformed Services University of the Health Sciences, Bethesda, MD 20184-4799, USA

Corresponding author: Cahoon, Edgar B (ecahoon2@unl.edu)

Current Opinion in Plant Biology 2013, **16**:350–357

This review comes from a themed issue on **Physiology and metabolism**

Edited by **John Browse** and **Edward Farmer**

For a complete overview see the Issue and the Editorial

Available online 14th March 2013

1369-5266/$ – see front matter, © 2013 Elsevier Ltd. All rights reserved.

http://dx.doi.org/10.1016/j.pbi.2013.02.009

Introduction

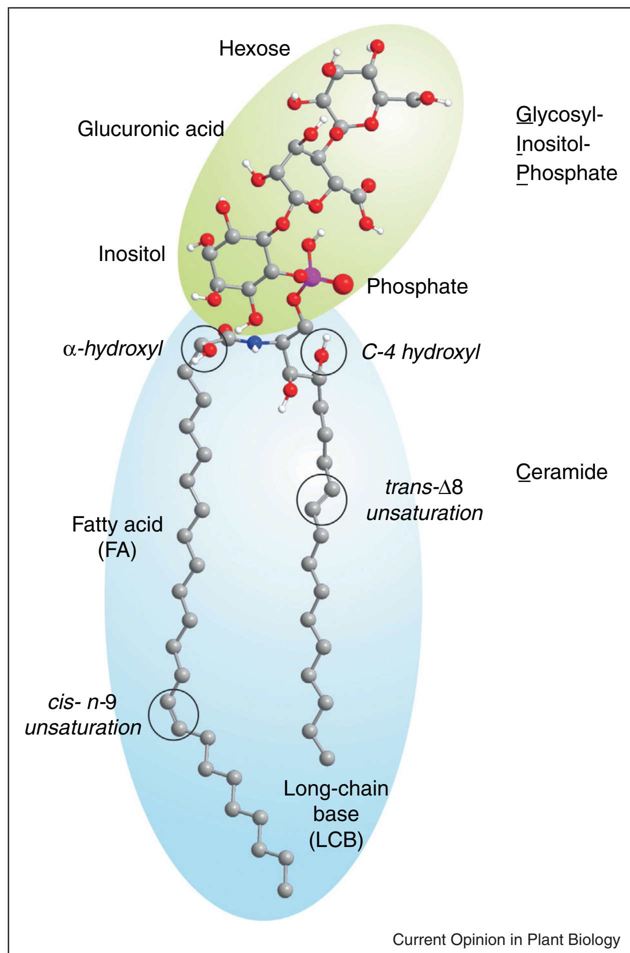
The metabolism and function of sphingolipids have gained increasing interest due to the recent appreciation of the quantitative significance of sphingolipids in specific membranes and their diverse roles in plant cells. Sphingolipids are ubiquitous in eukaryotes and have historically been studied in association with sphingolipid storage disorders such as Tay Sachs disease. In plants, sphingolipids are now recognized as major components of plasma membrane, tonoplast, and endomembranes. They exhibit substantial structural diversity, with hundreds of potential species, but until recently the significance of this structural complexity was unclear (Figure 1). Sphingolipids compose an estimated 40% of plasma membrane lipids and are enriched in the outer leaflet where they influence membrane integrity and ion permeability [1–3]. Sphingolipids are also intimately involved in endomembrane trafficking and are believed to function along with sterols and specific phospholipids in forming membrane domains (e.g. 'lipid rafts') [4–7]. Apart from their structural roles, sphingolipids are bioactive and participate in an array of processes and environmental responses such as programmed cell death (PCD) [8,9], pathogen-induced hypersensitive response (HR) [8,10•,11], ABA-dependent guard cell closure [12–14], host–pathogen interactions [15–17], and low-temperature signal transduction [18•,19,20]. Many of the structural modifications present in plant sphingolipids are distinct or absent from yeast and mammalian sphingolipids. Hence, the study of plant sphingolipids can provide insights into the importance of such structural diversity that is intractable in other eukaryotes. Mass spectrometry-based advances in analysis has provided a nearly complete 'sphingolipidome' of plant tissues [21] and the availability of Arabidopsis mutants has facilitated recent studies revealing the significance of sphingolipid structural complexity in controlling routes of metabolic flux and determining functional properties.

Sphingolipid structural complexity

Sphingolipid synthesis begins in the ER with condensation of serine and palmitoyl-CoA by serine palmitoyltransferase (SPT) (Figure 2) [22,23]. The product of this reaction is reduced to a C-1, C-3 dihydroxy C18 long-chain base (LCB), sphinganine, designated d18:0, indicating two hydroxyl groups (d), a chain length of 18-carbons (18), and no double bonds (0). Addition of a hydroxyl at C-4 produces the trihydroxy LCB, phytosphingosine or t18:0. LCBs may also be unsaturated by: (1) a *trans* double bond between C-4 and C-5 (or Δ4 position) of dihydroxy LCB and/or (2) a *cis* or *trans* double bond between C-8 and C-9 (or Δ8 position) of dihydroxy or trihydroxy LCB [24]. These structural variations mean that up to nine different LCB structures exist in plants. Both free LCBs and their C-1 phosphorylated derivatives (LCB-Ps) are present in plant cells at very low concentrations [21].

Additional sphingolipid structural complexity arises in the ceramide generated through amide linkage of a fatty acid (FA) to a LCB. The FA component of ceramide ranges in chain-length from C16 to C28, including odd-chain variants [24,25•], usually contain a C-2 or 'α-hydroxy' group, and can also contain a double bond at

Figure 1



A 3D, ball-and-stick representation of the predominant Arabidopsis sphingolipid highlighting structural modifications of particular interest (circles) discussed in the text. The glycosyl inositolphosphoceramide (GIPC) shown consists of a polar headgroup (enclosed in green) composed of phosphoinositol, presumably glucuronic acid based on structures from tobacco, and a final hexose. The precise conformation of the sugars and sugar linkages has yet to be determined for Arabidopsis. The ceramide portion (enclosed in blue) consists of a LCB that typically contains a C-4 hydroxyl and may contain a trans-Δ8 double bond (or unsaturation) linked via the nitrogen to a VLCFA, most commonly C24. The VLCFA of sphingolipids are mostly α-hydroxy fatty acids and in Arabidopsis, may contain a cis-n-9 unsaturation. Carbon atoms are shown in grey, oxygen in red, nitrogen in blue, phosphorous in purple and hydrogen in white: only polar hydrogen atoms are shown.

the n-9 position [26]. Similar to the LCB nomenclature, a saturated C24 fatty acid with α-hydroxylation is referred to as h24:0. The combination of 9 different LCBs and 32 different FAs yields 288 potential ceramides. Most (∼90%) sphingolipids in plants are in a ‘complex’ form with a polar headgroup linked to C-1 of the LCB ceramide. The polar headgroup and non-polar ceramide give complex sphingolipids their amphipathic and bilayer-forming properties [21,27]. One complex sphingolipid, glucosylceramide (GlcCer), comprises ∼30% of the sphingolipids in Arabidopsis leaves [21,27]. More abundant are the highly polar, anionic sphingolipids formed in the Golgi (Figure 2) with an inositolphosphate (IP) headgroup and up to 7 inositol-linked sugars collectively referred to as glycosyl inositolphosphoceramides (GIPCs) [21,28•,29]. In Arabidopsis, the most abundant GIPC, comprising ∼60% of leaf sphingolipids, contains a hexose-hexuronic acid linked to IPC [21]. Although 288 different ceramides could be associated with each headgroup [21], GlcCers and GIPCs *in planta* have distinctive ceramide compositions: GlcCers are enriched in dihydroxy LCBs and C16 FAs whereas GIPCs are enriched in trihydroxy LCBs and very-long chain (≥C20) FAs (VLCFAs) [1,27]. The mechanism underlying this segregation is unknown, but it highlights the complex role that structure plays in the metabolic routing of sphingolipids.

Significance of LCB and FA structures in sphingolipid metabolism and function

LCB hydroxylation and desaturation

The structural variability in plant LCBs arises from the activities of the LCB C-4 hydroxylase, Δ4 desaturase, and Δ8 desaturase (Figure 2). Recent characterization of Arabidopsis mutants lacking these enzymes has uncovered metabolic nuances of the sphingolipid biosynthetic pathway whereby LCB structure dictates downstream partitioning and ultimately determines the composition and content of total sphingolipids or specific sphingolipid classes [30••,31••,32]. These mutants have also allowed dissection of the significance of LCB hydroxylation and desaturation for plant growth and development.

In Arabidopsis, C-4 hydroxylation and Δ8 desaturation are quantitatively the most important, as ≥85% of the LCBs in leaf sphingolipids are trihydroxy as a result of the C-4 hydroxylase [encoded by *SBH1* (At1g69640) and *SBH2* (At1g14290)] [31••] and contain a *cis*-Δ8 or *trans*-Δ8 double bond arising from the Δ8 desaturase [encoded by *SLD1* (At3g61580) and *SLD2* (At2g46210)] [30••,33]. The LCB C-4 hydroxylase *sbh1*/*sbh2* double mutant, completely lacking trihydroxy LCBs, is severely dwarfed due to defects in both cell elongation and division and displays constitutive upregulation of HR PCD genes [31••]. Sphingolipidome analysis of *sbh1*/*sbh2* rosettes revealed hyper-accumulation of total sphingolipids to levels twofold to threefold higher than in wild type plants [31••], and the accumulated sphingolipids contained predominantly C16 FAs rather than the more typical C20–C26 VLCFAs. This phenotype suggested that sphingolipids with ceramides containing C16 FAs and dihydroxy LCBs are unable to support normal plant growth, and these sphingolipids or their metabolites are unable to regulate sphingolipid homeostasis [31••]. It also suggested two classes of ceramide synthases with different substrate specificities: one preferring C16 FAs and dihydroxy LCBs and the other VLCFAs and trihydroxy

Download English Version:

https://daneshyari.com/en/article/10869271

Download Persian Version:

https://daneshyari.com/article/10869271

Daneshyari.com