



Mini-review

Using lipidomics for expanding the knowledge on lipid metabolism in plants

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ABSTRACT

Lipids are a crucial and diverse class of biomolecules. Their structural heterogeneity in plants is staggering, and many aspects of plant life are manifested and mediated by lipids. Recent advances in metabolomic and lipidomic technologies and analysis have immensely increased our knowledge of the plant lipidome, its biosynthesis, regulation, adaptation, remodeling, functions, roles, and interactions. Here we review the recent literature and trends in lipidomics, and discuss specific issues pertaining to lipidomic research in plants, and how lipidomics has helped elucidate key issues in plant cell biology, immunity, response to stress, evolution, crop enhancement—to name but a few.

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1. Introduction

Lipids lie at the very definition of life. Membranes separate cells from each other, enclose organelles, and subdivide organelles into even smaller compartments. In this manner membranes generate a number of different environments within the cell in which different biochemical reactions occur. Aside from this important structural function, processes as fundamental for plants as photosynthesis or the electron transport chain in mitochondria occur in membranes; membranes in and of themselves therefore constitute an environment for biochemical reactions. Interestingly, separate environments—multiple domains with specific roles and a particular lipid and protein composition—exist within a membrane too. These domains are not static, can rather move through the surface of a membrane or blend into the membrane and later form again [1]. To add yet one more level of complexity, the lipid bilayer is not symmetrical: it contains different kinds of lipids on each of the leaflets, possibly due to the different conditions to which the membrane can be exposed on both sides [1]. This bilayer asymmetry, the domains within membranes, and indeed the entire membrane diversity existing in a single cell, are the product of an active lipid metabolism. Lipids forming the membranes of plant cells are constantly

being produced and degraded, portions of lipids can be recycled, and there is extensive trafficking between different organelles.

Plant biochemists have been studying this fascinating nature of lipids for more than 30 years. Initially the main focus was to understand how lipids were synthesized and transformed. Radio-labeling studies indicated the sequence in which fatty acids were produced, incorporated into glycerolipids, and desaturated. In 1982, Roughan and Slack [2] systematized the evidence coming from those studies and pointed out a major conclusion: plant glycerolipids are produced by two discrete pathways, one taking place in the chloroplast (the prokaryotic pathway) and another one in the endoplasmic reticulum (ER; the eukaryotic pathway). The emergence of *Arabidopsis thaliana*, which possesses both pathways, as a genetic model, enabled the dissection of lipid-biosynthesis regulation. Mutagen screenings carried out on this species allowed to identify mutants for most fatty-acid desaturases and several other mutants with a drastic phenotype in lipid composition [3]. These studies revealed that most desaturation steps in plants occur once fatty acids are already bound to membrane lipids. Remarkably, the authors uncovered that the loss of a given function in either the chloroplast or the ER pathway would trigger compensation by the other pathway. At this point, however, most genes involved in these pathways remained unknown. In the 1990s, the molecular-biology boom allowed to characterize an important number of genes spread all across lipid metabolism. Map-based cloning allowed to find the genes coding for most desaturases found previously in mutagen screenings [4], and of other important

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lipid biosynthetic genes. Particular progress was made on the galactolipid pathway [5]. The cloning of MGD1 and DGD1 sequences, the two main galactosylases in *Arabidopsis*, allowed to reconstitute the plant galactolipid biosynthetic pathway in *Escherichia coli* [6].

The completion of the *Arabidopsis* genome sequencing [7] boosted the discovery of an unprecedented number of genes involved in lipid metabolism [8]. By querying the genome with known genes from other organisms it was often possible to find the *Arabidopsis* ortholog. It thus became possible to obtain a fairly complete picture of most genes involved in lipid synthesis. The pathways explored included not only membrane glycerolipids—traditionally the main focus of lipid biochemistry—but also sphingolipids, the storage lipid triacylglycerol, cutin, waxes and suberin. Electronic databases have been created in order to contain the huge amount of generated data (for instance, in plants: [9]).

The rise of high-throughput genomic, transcriptomic and metabolomic tools heralded the era of omics. Lipidomics, a field within metabolomics, aims to analyze simultaneously as many as possible lipid compounds in a given sample—and ideally, eventually, all of them. More than a decade after the first lipidomic study [10], we shall present recent key contributions of lipidomics to different aspects of plant lipid research (Fig. 1) and review developments and trends in the field.

2. Modern lipidomics: the birth and rise of a new field

Great technological strides have been achieved since the early days of lipid characterization.

While the traditional method of choice, namely thin-layer chromatography (TLC) in conjunction with gas chromatography (GC), is still widely used, today's methods are truly high-throughput, and enable the analysis of lipids without prior degradation to their fatty-acid components.

Wolti and colleagues [10], in their formative lipidomic characterization of phospholipase D α 's (PLD α) role in freezing tolerance, directly infused lipid extracts into a mass spectrometer (MS), a methodology that is still utilized nowadays ([11,12]). An alternative

to direct infusion was developed employing liquid-chromatographic (LC) separation prior to MS [13]. This reduced problems such as limited sensitivity of low-abundance species, and significantly improved the resolution for compounds with identical masses. Improved methods, often specifically developed for plant lipidomics, sprout continually: some address the general aspiration to detect as many lipid classes and species as accurately as possible and using as few analytical steps as possible [14]; while other focus on specialized topics, such as the spatial localization of lipids in plant tissues using lipidomics [15]. Biological significance is becoming more and more prominent in lipidomic studies, with mere “grocery” lists of lipids becoming a rarity. Even the authors of technical-advance reports make sure to apply their advance to real-life biology. Tarazona and co-workers [14], for instance, utilized their enhanced LC–MS-based method to analyze lipid changes in cold- and drought-stressed plants, coming up with a record number of 393 species in 23 lipid classes and providing novel insights for the involvement of sphingolipids and sterols in these stresses. Indeed, several lipidomic endeavors were specifically dedicated to the two latter classes: sterols were catalogued and quantified comprehensively for the first time in plants only recently [16], and sphingolipids four years earlier [17].

3. Beyond membranes

Aside from the important structural function of lipids, most prominently in membranes, plant lipidomic analysis has been used to research their other biological functions as well. When considering oil production in plants, for instance, a topic of current relevance that involves mainly the accumulation of triacylglycerols (TAGs), single-cell analysis enabled their direct *in vivo* profiling in green microalgae, sparing the need for extraction and providing real-time data [18]. A comprehensive systems approach comprising of global lipidomic and transcriptomic profiling was employed for the elucidation of oil-synthesis mechanisms in algae [19]. Industrial applications aside, lipid profiling is often exercised in nutritional research, where it is used, among others, to monitor the success of

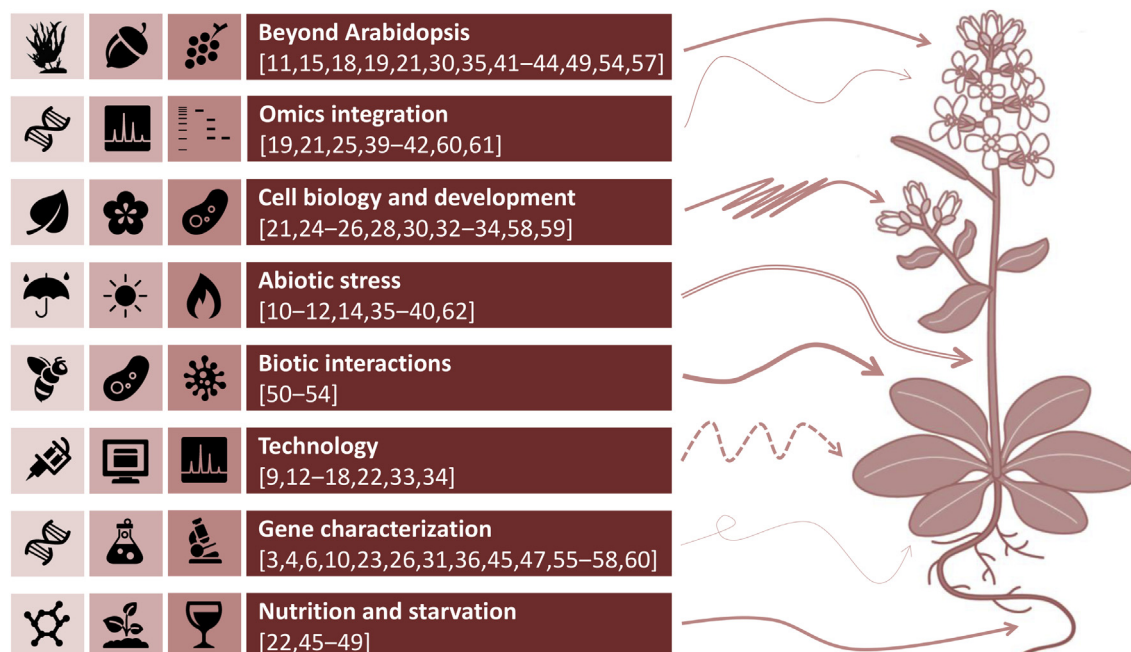


Fig. 1. A graphic summary of some of the topics discussed in this review, along with the relevant references. All icons taken from www.icons8.com.

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