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REVIEW PAPER

Lipid droplet proteome plasticity in plant evolution, growth and development, and response to stress

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Abstract

Lipid droplets (LDs) are subcellular structures that occur in all plant cells and are composed of a core of hydrophobic molecules, such as triacylglycerols, surrounded by a phospholipid monolayer and various associated proteins. In recent years, proteomic studies have significantly increased the number of known LD proteins, revealing that the LD proteins that predominate in seeds already evolved in streptophyte algae. In multicellular plants, there are distinct differences across tissues regarding the composition of the LD proteome. There are also dynamic changes in the LD proteome during developmental processes, such as seedling establishment and senescence, and in response to abiotic and biotic stresses. Overall, the success of these proteomics studies has come not only from cataloging of LD protein compositions, but also the identification of previously unknown LD protein families. As a result, these studies have provided the framework for the functional characterization of LD proteins and their wide-ranging roles in LD biogenesis and degradation, metabolism, and during stress. In this review, we highlight the main differences in the LD proteomes across plant species, tissues, development and/or environmental factors, and provide descriptions of some of the key physiological and subcellular functions of the individual families of LD proteins.

Keywords: Abiotic stress, biotic stress, development, evolution, lipid droplets, lipid metabolism, proteomics.

Abbreviations: 2-HOT, 2, HYDROXY OCTADECATRIENOIC ACID; ABA, abscisic acid; ABI-1, ABSCISIC ACID INSENSITIVE 1; α-DOX1, α-DIOXYGENASE 1; CAS, CYCLOARTENOL SYNTHASE; CDC48, CELL DIVISION CYCLE 48; CLO, CALEOSIN; ERD7, EARLY RESPONSIVE TO DEHYDRATION 7; GPAT, GLYCEROL-3-PHOSPHATE ACYLTRANSFERASE; HISE1, HIGH STEROL ESTER 1; LD, lipid droplet; LDAF1, LD ASSEMBLY FACTOR 1; LDAP, LD-ASSOCIATED PROTEIN; LDIP, LDAP-INTERACTING PROTEIN; LDS1, LDs AND STOMATA 1; LIME1, LD METHYLTRANSFERASE 1; LOX, LIPOXYGENASE; MLDP, MAJOR LD PROTEIN; OBL, OIL BODY LIPASE; OLE, OLEOSIN; OSC, OXIDOSQUALENE CYCLASES; PUX10, PLANT UBX DOMAIN-CONTAINING PROTEIN 10; SDP1, SUGAR DEPENDENT 1; TAG, triacylglycerol; TGD1, TRIGALACTOSYLDIACYLGLYCEROL 1; VAMP, VESICLE-ASSOCIATED MEMBRANE PROTEIN; VAP27-1, VAMP-ASSOCIATED PROTEIN 27-1.

Introduction

Lipid droplets (LDs) are unique cytosolic organelles that are ubiquitous in eukaryotes. Their most distinguishing features are the lipid monolayer and nonpolar core, the latter containing storage lipids, like triacylglycerol (TAG), and other hydrophobic compounds, such as fatty acid steryl esters and other terpenoids (Zhou *et al.*, 2019; Guzha *et al.*, 2023; Scholz *et al.*, 2026). In plants, cytosolic LDs are distinct from plastoglobules, which share the same basic structure but occur in the plastidial stroma and are often connected to the thylakoid membrane. For an extensive review on plastoglobuli, refer to Lundquist *et al.* (2020) and van Wijk and Kessler (2017).

LDs originate from the endoplasmic reticulum membrane. Here, triacylglycerol (TAG) molecules are inserted between the membrane leaflets during their synthesis by acyltransferases and accumulate into a so-called lipid 'lens', which subsequently bulges out towards the cytosol (Ischebeck *et al.*, 2020). According to current models for LD biogenesis that are considered to apply to plants, fungi, and animals alike, the initiation of the lipid lens and the subsequent formation of the nascent LD is orchestrated, at least in part, by SEIPIN family proteins, which form a multimeric, ring-like structure at the connection between the endoplasmic reticulum and nascent LD (Wang *et al.*, 2016; Arlt *et al.*, 2022; Scholz *et al.*, 2022).

In Arabidopsis, a loss of the three SEIPIN paralogs results in plants that are still able to synthesize LDs, but they are of larger, more inhomogeneous size, and hampered in their functionality (Cai *et al.*, 2015; Taurino *et al.*, 2018). Arabidopsis SEIPINs 2 and 3 have been also shown to interact with VESICLE-ASSOCIATED MEMBRANE PROTEIN (VAMP)-ASSOCIATED PROTEIN 27-1 (VAP27-1), as well as LIPID DROPLET-ASSOCIATED PROTEIN (LDAP)-INTERACTING PROTEIN (LDIP) (Greer *et al.*, 2020; Guzha *et al.*, 2023), the latter of which also interacts with the structural LD surface proteins LDAP1, 2, and 3 (Pyc *et al.*, 2021). Additionally, new data suggest that SEIPIN family proteins interact with the small G protein LIPID DROPLETS AND STOMATA 1 (LDS1)/RABC1, which in turn interacts with ABSCISIC ACID INSENSITIVE1 (ABI1) (Ge *et al.*, 2022; Wang *et al.*, 2025). Similar to the *seipin* mutants, Arabidopsis lines disrupted in *VAP27-1* or *LDIP* harbor enlarged LDs (Pyc *et al.*, 2017; Greer *et al.*, 2020), while disruption of *LDS1* leads to severe defects in guard cell vacuole morphology and stomatal function (Ge *et al.*, 2022).

The degradation of TAG stored in LDs, followed by the uptake of fatty acids into peroxisomes and their breakdown by β-oxidation during germination, is well described (Zolman *et al.*, 2001; Fulda *et al.*, 2002; Eastmond, 2006; Thazar-Poulot *et al.*, 2015; Cui *et al.*, 2016). Further, the required tight spatial interplay of LDs, peroxisomes (i.e. glyoxysomes) and the endoplasmic reticulum during LD mobilization has recently been studied in detail by cryo-scanning electron microscopy of Arabidopsis seedlings throughout establishment (Wanner *et al.*, 2025). Here, the critical physiological function of LDs is clear: their stored TAG serves as a source of energy and carbon, which is mostly required by the developing seedling for the synthesis of cell walls and for the *de novo* synthesis of lipids to reconstitute the membranes of the photosynthetic apparatus (Le Moigne *et al.*, 2022).

In other tissues, such as pollen tubes, TAG-derived acyl chains might also serve as building blocks for membrane lipids (Ischebeck, 2016). Additionally, LDs in plants could be a source for sterols in membranes, as LD-stored sterol esters are degraded during heat stress in leaves and roots (Scholz *et al.*, 2024, 2026). Here, LDs simultaneously act as a sink organelle, when membrane lipids are degraded and remodeled, and the released acyl chains are channeled into LDs in the form of TAG.

Apart from these roles in primary metabolism, LDs in plants have been also implicated in pathogen defense in leaves (Shimada *et al.*, 2014), in guard cell development (Ge *et al.*, 2022), as hubs for triterpene synthesis and storage in Arabidopsis roots and leaves of tea plants (*Camellia sinensis*) (Zhou *et al.*, 2019; Scholz *et al.*, 2026), and possibly the synthesis of furan-ring-containing fatty acids (Omata *et al.*, 2024). Overall, this remarkable diversity of functions at LDs across species, tissues, and environmental conditions manifests itself in a highly variable and adjustable LD proteome. In this review, we survey previously published proteomics datasets and highlight these distinct differences and changes in the protein compositions of LDs in plants, and discuss their allied LD functions.

Proteomics—paving the way for understanding lipid droplet function

Proteomic studies of specific subcellular structures and organelles can be a key aspect of elucidating their functions. As such, obtaining an effective way to fractionate the contents of the cell before the proteomic analysis is a crucial first step. For LDs, this is usually achieved by (ultra-)centrifugation, utilizing the low density of the stored oil in LDs in order to separate them from other cellular contents (Horn *et al.*, 2021; Xu *et al.*, 2023; Omata *et al.*, 2024). While this can be a very effective method, there are several points that can render enrichment and subsequent analysis challenging. One such challenge is a relatively low number of LDs found in most vegetative tissues (leaves, stems, roots, etc.), which makes it more difficult to obtain a sufficient LD fraction for proteomic analysis. In addition, plastoglobuli have similar biophysical properties and can contaminate the (cytosolic) LD fraction if plastid integrity is disrupted during the LD isolation procedure.

To help overcome these issues and aid LD enrichment from more challenging vegetative tissues, such as leaves, LD number can be increased by subjecting plants to specific abiotic stress

conditions or studying them during senescence (Brocard *et al.*, 2017; Doner *et al.*, 2021; Omata *et al.*, 2024). A second option is genetic manipulation. For example, the Arabidopsis double mutant line *tgd1-1 sdp1-4* (*trigalactosyldiacylglycerol 1*, *sugar dependent 1*) and the mutant line *hise1-2* (*high sterol ester 1*) have strongly increased levels of TAG and sterol esters, respectively (Fan *et al.*, 2014; Shimada *et al.*, 2019), and thus both accumulate LDs. The use of transgenic lines and stress conditions, such as heat stress or infection with *Botrytis cinerea* or *Pseudomonas syringae*, can also be combined in order to aid in LD enrichment for proteomic analyses (Scholz *et al.*, 2024). This also has the added advantage of not only providing a unique stress-induced LD proteome dataset, but also yielding data from a parallel control treatment that does not normally lead to a sufficient LD accumulation on its own. While a caveat is that the use of different mutant lines, LD isolation protocols, and/or proteomic methodologies limits the comparability of different studies, general observations can still be made. Furthermore, studies of LDs have often also highlighted proteins that hitherto were not known to be associated with the organelle. These discoveries are especially valuable if combined with research studies aimed at confirming the subcellular localization of these putative LD proteins. For instance, the respective candidate LD protein can be tagged with a fluorophore and transiently expressed in an ectopic expression system, such as *Nicotiana benthamiana* leaves (Brocard *et al.*, 2017) or *N. tabacum* pollen tubes (Müller *et al.*, 2017). Thereafter, by correlating the sublocalization pattern with LD staining, using neutral specific dyes, such as Nile red or BODIPY (4,4-difluoro-4-bora-3a,4a-diaza-*s*-indacene) derivatives, it is possible to confirm the LD localization of the respective protein(s). Indeed, to date, this experimental approach has resulted in the discovery of 42 LD protein families in Arabidopsis, containing more than 70 individual proteins (Table 1).

We performed a meta-analysis of the abundance of these 42 LD protein families across 42 different sample types of various species, tissues treatments and developmental stages derived from 16 separate studies (Ischebeck *et al.*, 2014; Brocard *et al.*, 2017; Kretzschmar *et al.*, 2018, 2020; Stavrinides *et al.*, 2020; Doner *et al.*, 2021; Karagiannis *et al.*, 2021; Veerabagu *et al.*, 2021; Niemeyer *et al.*, 2022; Dadras *et al.*, 2023; Stout *et al.*, 2023; Hembach *et al.*, 2024; Scholz *et al.*, 2024, 2026; Torres-Romero *et al.*, 2024; Galindo-Lujan *et al.*, 2025) (Supplementary Table S1; Supplementary Dataset S1). More specifically, we compared the data in these studies by reanalysing all the raw data using MaxQuant software (version 2.0.3.1) with the same settings (as outlined in Supplementary Dataset S1). We then calculated the relative abundance of the proteins among all LD proteins based on the intensity-based absolute quantification (iBAQ) algorithm, which indicates molar protein levels by dividing the sum peak intensity by all theoretically observable peptides (Schwanhausser *et al.*, 2011). When further dividing the iBAQ by the abundance of all observed proteins, we obtained the relative iBAQ (riBAQ) values, which were used in this study. Since we assumed that the proteins within the 42 analysed individual protein families have similar molecular functions, we added the abundance of all the proteins within each family. Of these families, six were categorized as highly abundant (relative abundance >10% of all LD proteins) in one or more of the analysed LD enriched data sets and the other 36 were defined as low-abundance protein families. Across all sample types, no two LD proteomes were alike, indicating that they are adapted to the individual needs of the organism, tissue, developmental stage, and/or environmental conditions (Figs 1–5; Supplementary Dataset S1).

Lipid droplet proteomes of seeds and their plasticity during seedling establishment

In most seed plants, LDs are highly prominent in embryonic tissues (Chapman *et al.*, 2012) and, to a lesser extent, in pollen (Rotsch *et al.*, 2017). However, as mentioned earlier, LDs also occur, albeit in lower amounts, in vegetative tissues, such as roots (Scholz *et al.*, 2026) and leaves (Pyc *et al.*, 2017), including specialized cells, like guard cells (Ge *et al.*, 2022). In these tissues or cells, the number and size of LDs can increase under abiotic stresses or senescence (Gidda *et al.*, 2016; Brocard *et al.*, 2017). Furthermore, they can also accumulate under regular conditions in certain vegetative tissues, such as the buds of hybrid aspen (*Populus trichocarpa*) (Veerabagu *et al.*, 2021) and the oil-rich tubers of yellow nutsedge (*Cyperus esculentus*) (Turesson *et al.*, 2010) or mesocarp of avocado (Horn *et al.*, 2013).

In seeds, LDs are crucial as a source of energy and carbon to facilitate seedling establishment under favorable conditions (Eastmond, 2006). During extended times of seed desiccation and potentially under other harsh environmental conditions, the resources stored within LDs must be preserved. To ensure their proper function, LDs also have to be prevented from fusing with each other (Siloto *et al.*, 2006; Shimada *et al.*, 2008), while the TAG stored in LDs has to be protected from oxidation (Smirnoff, 2010).

To highlight which protein families appear especially important for seed LD integrity and function, we compared the seed LD protein composition from five different plant species (Fig. 1). For Arabidopsis (Kretzschmar *et al.*, 2020) and tobacco (*N. tabacum*) (Kretzschmar *et al.*, 2018), the proteomics data analysed were obtained from isolated LD fractions. For soybean (*Glycine max*; Stout *et al.*, 2023), coffee (*Coffea arabica*; Stavrinides *et al.*, 2020), and quinoa (*Chenopodium quinoa*; Galindo-Lujan *et al.*, 2025), the data were obtained from total cellular protein extracts. While the latter data were less preferable than those from isolated LDs, LDs are likely a dominant organelle within the seeds of these three species. Hence, we are confident a valid representation of the relative composition of the LD proteome can be estimated from the total cellular proteomes.

Table 1 LD-associated protein families from Arabidopsis

Description/protein name	Abbreviation	AGI codes	Function	Publication
Aldehyde dehydrogenase	ALDH4	AT1G44170	Unknown	Scholz *et al*. (2026)
α-Dioxygenase	α-DOX1	AT3G01420	Oxylipin biosynthesis	Shimada *et al*. (2014)
Cycloartenol synthase	CAS	AT2G07050	Sterol metabolism	Kretzschmar *et al*. (2018)
Cytochrome b_5 isoform	CB5-E	AT5G53560	Unknown	Scholz *et al*. (2024)
Caleosins	CLO	AT4G26740, AT5G55240, AT2G33380, AT1G70670, AT1G70680, AT5G29560, AT1G23250, AT1G23240	Stress responses	Chen *et al*. (1999)
EARLY RESPONSIVE TO DEHYDRATION 7	ERD7	AT2G17840	Lipid remodelling under stress	Doner *et al*. (2021)
FOREVER YOUNG 3	FEY3	AT4G27760	Putative oxidoreductase	Scholz *et al*. (2026)
Glycerol-3-phosphate 2-*O*-acyltransferase	GPAT 1 to 8	AT1G01610	Cutin biosynthesis	Fernández-Santos *et al*. (2020)
Glycerol-3-phosphate 1-*O*-acyltransferase	GPAT9	AT5G60620	Kennedy pathway	Scholz *et al*. (2026)
Steroleosin, hydroxysteroid dehydrogenases	HSD	AT5G50600, AT5G50700, AT3G47350, AT3G47360, AT5G50590, AT4G10020, AT5G50770, AT5G50690	Sterol- and NADP-binding motifs, Brassinosteroid metabolism	Lin *et al*. (2002)
Lipid droplet associated hydrolase	LDAH	AT1G10740, AT1G23330	Metabolism	Kretzschmar *et al*. (2020)
LD associated Protein	LDAP	AT1G67360, AT2G47780, AT3G05500	Surfactant, LD formation	Horn *et al*. (2013)
Lipid droplet dehydrogenase	LDDH	AT1G75180, AT1G19400	Metabolism	Kretzschmar *et al*. (2020)
LDAP interacting protein	LDIP	AT5G16550	LD formation	Pyc *et al*. (2017)
LD-localized NTF2 family protein	LDNP	AT5G04830	Unknown	Scholz *et al*. (2024)
Lipid droplet protein of seeds	LDPS	AT3G19920	Regulation of LD size	Kretzschmar *et al*. (2020)
LIPID DROPLETS AND STOMATA 1	LDS1/RABC1	AT1G43890	Guard cell development	Ge *et al*. (2022)
LEAF WILTING 1	LEW1	AT1G11755	Terpene metabolism	Scholz *et al*. (2026)
LD lipase	LIDL	AT1G18460, AT1G73920	Putative lipase	Kretzschmar *et al*. (2020)
LD methyltransferase	LIME	AT4G33110, AT4G33120	Putative role in furan fatty acid metabolism	Kretzschmar *et al*. (2020)
LD plasma membrane adaptor	LIPA	AT1G07985	LD plasma membrane tethering	Krawczyk *et al*. (2022)
Lysophospholipid acyltransferase	LPEAT1	AT1G80950	Membrane lipid metabolism	Scholz *et al*. (2026)
Marneral synthase	MRN1	AT5G42600	Terpene metabolism	Scholz *et al*. (2026)
Myosin binding protein	MYOB14	AT4G13160	Myosin binding	Omata *et al*. (2024)
Oil body lipase	OBL	AT3G14360, AT5G67050, AT1G45201, AT1G56630, AT5G42930	Lipid and volatile metabolism	Eastmond (2004)
Oleosins	OLE	AT4G25140, AT5G40420, AT5G51210, AT3G27660, AT3G01570, AT1G48990, AT2G25890, AT3G18570	Surfactant, LD formation	Qu *et al*. (1986)
Protein associated with lipid droplets	PALD	AT1G67540	Pollen longevity	Li *et al*. (2022)
Prenylcysteine methylesterase	PCME	AT5G15860	Unknown	Scholz *et al*. (2026)
UBX domain-containing protein	PUX10	AT4G10790	Protein degradation	Kretzschmar *et al*. (2018)
Sugar dependent type TAG lipase	SDP1	AT5G04040, AT3G57140	Triacylglycerol degradation	Eastmond (2006)
Seipin	SEIPIN	AT5G16460, AT1G29760, AT2G34380	LD formation	Cai *et al*. (2015)
Seed lipid droplet protein	SLDP	AT1G65090, AT5G36100	LD plasma membrane tethering	Kretzschmar *et al*. (2020)
Sterol methyltransferase	SMT1	AT5G13710	Sterol metabolism	Kretzschmar *et al*. (2018)

(*continued*)

Table 1 Continued

Description/protein name	Abbreviation	AGI codes	Function	Publication
Thalianol synthase	THAS1	AT5G48010	Terpene metabolism	Scholz *et al*. (2026)
Unsaturated fatty acid methyl-transferase/dehydrogenase	UFAM1/ UFAD1	AT3G23510	Putative role in furan fatty acid metabolism	Omata *et al*. (2024)
Unsaturated fatty acid oxidase	UFAO1	AT1G30130	Putative role in furan fatty acid metabolism	Omata *et al*. (2024)
VAMP-associated protein	VAP27-1	AT3G60600	LD formation	Greer *et al*. (2020)
Glycosyl transferase family		AT1G78800, AT1G16570	Unknown	Scholz *et al*. (2026)
Putative hydrolase		AT4G33180	Unknown	Scholz *et al*. (2026)
Putative short-chain dehydrogen-ase/reductase		AT5G04070	Unknown	Scholz *et al*. (2026)
Putative short-chain dehydrogen-ase/reductase		AT5G10050	Unknown	Scholz *et al*. (2026)
Protein of unknown function		AT5G59960	Unknown	Scholz *et al*. (2026)

According to the combined proteomics results that we obtained, LD proteins constitute between 0.2% in soy and 5.7% in Arabidopsis of the total proteome, while the oil content varies between 5.3% for quinoa and 36% in Arabidopsis (Wood *et al*., 1993; O'Neill *et al*., 2003; Stanisavljevic *et al*., 2007; Dong *et al*., 2021; Liu *et al*., 2022) (Fig. 1A). The most abundant LD proteins in the seeds of all five species are oleosins, steroleosin [also referred to as hydroxysteroid dehydrogenases (HSDs)] and caleosins (Fig. 1A), which is consistent with the literature (Huang, 1992; Chen *et al*., 1999; Lin *et al*., 2002). However, the ratios of these LD proteins can differ considerably from species to species. For example, while oleosins always represent the major portion of LD proteins at around 60–70%, either caleosins in tobacco or steroleosins in quinoa, coffee, and Arabidopsis form the second most abundant protein group at 25–30%. The respective other protein families constitute the last 4–8% (Fig. 1B; Supplementary Data S1), the exception being soy seed LDs, which are almost exclusively oleosins (i.e. 96% of all LD proteins).

Oleosins are considered structural LD proteins characterized by a hydrophobic hairpin structure with a proline knot at the hairpin bend. Based on this structure, the protein is considered to be anchored into the lipid monolayer and hydrophobic core of the LD (Tzen *et al*., 1992). In Arabidopsis, there are eight oleosin homologs and all are found in seeds in varying amounts (Kretzschmar *et al*., 2020). Oleosins are postulated to prevent the LDs from fusing when packed closely together. This is supported by results obtained with *ole1-1* knock out mutants, where LDs are much larger, even though only one of the homologs is disrupted (Siloto *et al*., 2006). Moreover, if additional oleosin proteins are absent, LDs are even larger in diameter (Shimada *et al*., 2008). Oleosins are also postulated to protect seeds from freezing stress since single mutant lines of *OLEOSIN1*, *2*, or *3* display a lower germination rate if subjected previously to temperatures of −30 °C, while seeds of double mutants *ole-1 ole-2* and *ole-1 ole-3* fail to germinate at all.

The family of eight HSDs in Arabidopsis are considered to function as steroid dehydrogenases, as HSD1 was shown to be active for 17β-hydroxysteroids, such as cortisol (d'Andrea *et al*., 2007). However, the native substrates of HSDs in plants are not known. One possibility is that HSDs are important in the metabolism of brassinosteroids (Chapman *et al*., 2012), which are plant hormones that regulate seed dormancy, plant growth, and development (Zebosi *et al*., 2024). Support for this premise comes from observations that the overexpression of *HSD1* in Arabidopsis results in decreased seed dormancy (Li *et al*., 2007; Baud *et al*., 2009) and taller Arabidopsis plants with an increased number of stems, which mirrors exogenous brassinosteroid treatment (Li *et al*., 2007). HSDs at LDs could therefore be important to modulate brassinosteroid effects on seed dormancy and seedling growth, but additional studies, perhaps using higher-order *hsd* knockout lines, which to our knowledge have not yet been developed, will be needed to investigate this possibility.

In Arabidopsis, caleosins form a family of eight proteins and were originally described as having a similar hairpin and proline knot structure as oleosins (Chen *et al*., 1999). However, in contrast to oleosins, this structural feature is not supported by publicly available AlphaFold2 predictions (Jumper *et al*., 2021). Caleosins are also predicted to contain a calcium-binding EF hand motif (Chen *et al*., 1999; Naested *et al*., 2000) and a peroxygenase function (Hanano *et al*., 2023) that acts on lipid peroxides. In Arabidopsis leaves, CALEOSIN3 is associated with a protective function against biotic (Shimada *et al*., 2015) and abiotic stress (Aubert *et al*., 2010). In seeds, however, CALEOSIN1 and 2 are the predominant members of the protein family (Kretzschmar *et al*., 2020). Assuming all caleosins share a similar enzymatic function, it is possible that these proteins provide cellular protection during desiccation and seedling establishment by detoxifying lipid peroxides that can accumulate during seed aging (Sung and Jeng, 1994; Sung and Chiu, 1995).

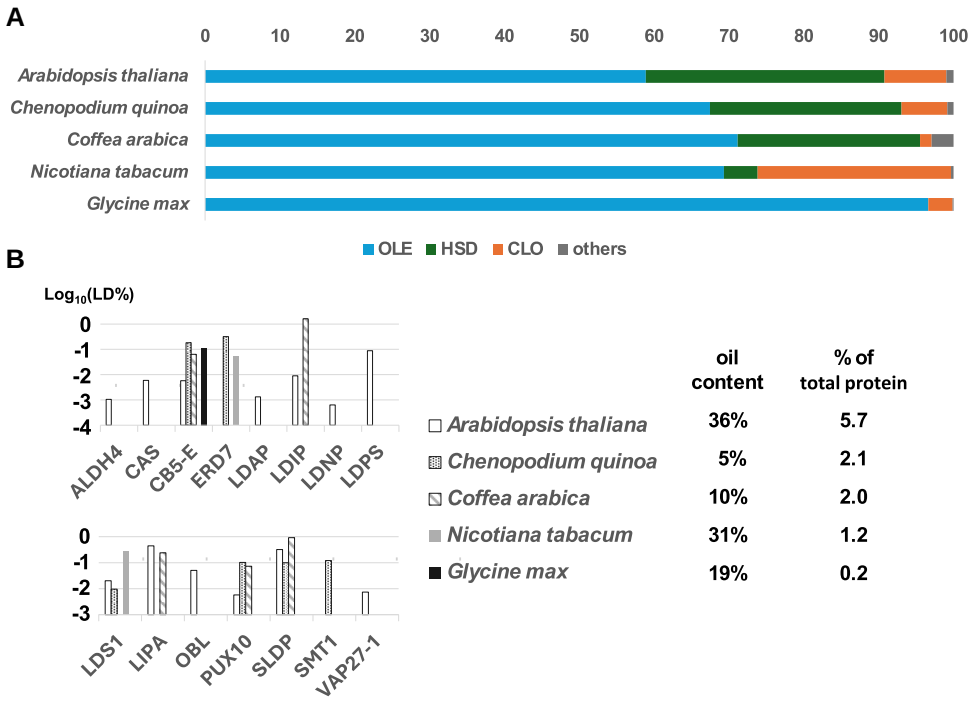

Fig. 1. The seed lipid droplet (LD) proteome differs among species but is dominated by oleosin in all displayed cases. Relative abundances [molar ratios of proteins as percentage based on relative intensity-based absolute quantification (riBAQ)] of LD proteins in seed proteomes of five different plant species are compared. For Arabidopsis and *Nicotiana tabacum*, data derive from LD enriched fractions while they are taken from total cellular extracts of the other species. (A) The most abundant proteins; (B) the lower abundant proteins, the oil content, and the proportion of all LD proteins in the total cellular proteome. The scale was set to depict all measured data points. The absence of bars indicates protein families that were not detected in the sample. Abbreviations: ALDH4, Aldehyde dehydrogenase; CAS, cycloartenol synthase; CB5-E, cytochrome b_5 isoform; CLO, caleosin; ERD7, EARLY RESPONSIVE TO DEHYDRATION 7; HSD, hydroxysteroid dehydrogenases, steroleosin; LDAP, LD associated protein; LDIP, LDAP interacting protein; LDNP, LD-localized NTF2 family protein; LDPS, Lipid droplet protein of seeds; LDS1/RABC1, LIPID DROPLETS AND STOMATA 1; LIPA, LD plasma membrane adaptor; OBL, oil body lipase; OLE, oleosins; PUX10, plant UBX domain-containing protein; SLDP, seed lipid droplet protein; SMT1, Sterol methyltransferase; VAP27-1, VAMP-associated protein. Proteomic data derive from Galindo-Lujan *et al*. (2025), Kretzschmar *et al*. (2018, 2020), Stout *et al*. (2023), and Stavrinides *et al*. (2020), and lipid data from Dong *et al*. (2021), Liu *et al*. (2022), O'Neill *et al*. (2003), Stanisavljevic *et al*. (2007), and Wood *et al*. (1993).

A fourth major plant LD protein family, comprising the LD-ASSOCIATED PROTEINs (LDAPs), is not as abundant in seeds, but is more prominent in vegetative tissues. This protein family in Arabidopsis consists of three proteins that, akin to oleosins, are considered to have a structural role as an LD 'coat' protein (Horn *et al*., 2013; Gidda *et al*., 2016; Kim *et al*., 2016). In addition, LDAPs, along with SEIPINs and LDAP-INTERACTING PROTEIN (LDIP), participate in the control of nascent LDs budding from the endoplasmic reticulum membrane (Pyc *et al*., 2021; Clews *et al*., 2025; Whitehead *et al*., 2025). Perhaps due to this latter function, *ldap-1* mutant lines are disrupted in the separation of LDs from the endoplasmic reticulum leading to the observed increased LD sizes in seedlings via the constant filling of TAG into the LD core (Gidda *et al*., 2016).

Apart from the abovementioned four major LD protein families (i.e. OLEOSINs, CALEOSINS, HSDs, and LDAPs), numerous less abundant proteins are also associated with seed LDs. However, since the total protein extracts reach the detection limit, only the Arabidopsis proteomics data can be discussed. Herein, two protein families are almost exclusively found in developing and mature seeds, and seedlings, namely SEED LD PROTEIN 1 and 2 (SLDP1/2), and LD PROTEIN OF SEEDS (LDPS) (Kretzschmar *et al*., 2020). SLDP1/2 bind to LDs and interact with the plasma membrane-associated protein LIPID DROPLET PLASMA MEMBRANE ADAPTOR (LIPA) (Krawczyk *et al*., 2022). This interaction constitutes a membrane contact site that tethers LDs to the plasma membrane, causing LDs to align at the cell membrane of cotyledon and hypocotyl cells of Arabidopsis seedlings. In mutant lines missing either LIPA or both SLDPs, this tethering and, by extension, cellular LD organization overall, is disrupted. Notably, despite this striking change in cellular organization of LDs in these mutant lines, seedling establishment and TAG breakdown are not obviously affected and the physiological role(s) of the LIPA/SLDP-mediated contact site remains to be identified (Krawczyk *et al*., 2022; Scholz *et al*., 2022).

Another notable LD protein identified in Arabidopsis is LDPS, which is exclusively found in the LD proteomes of development stages from siliques to seedlings and has been

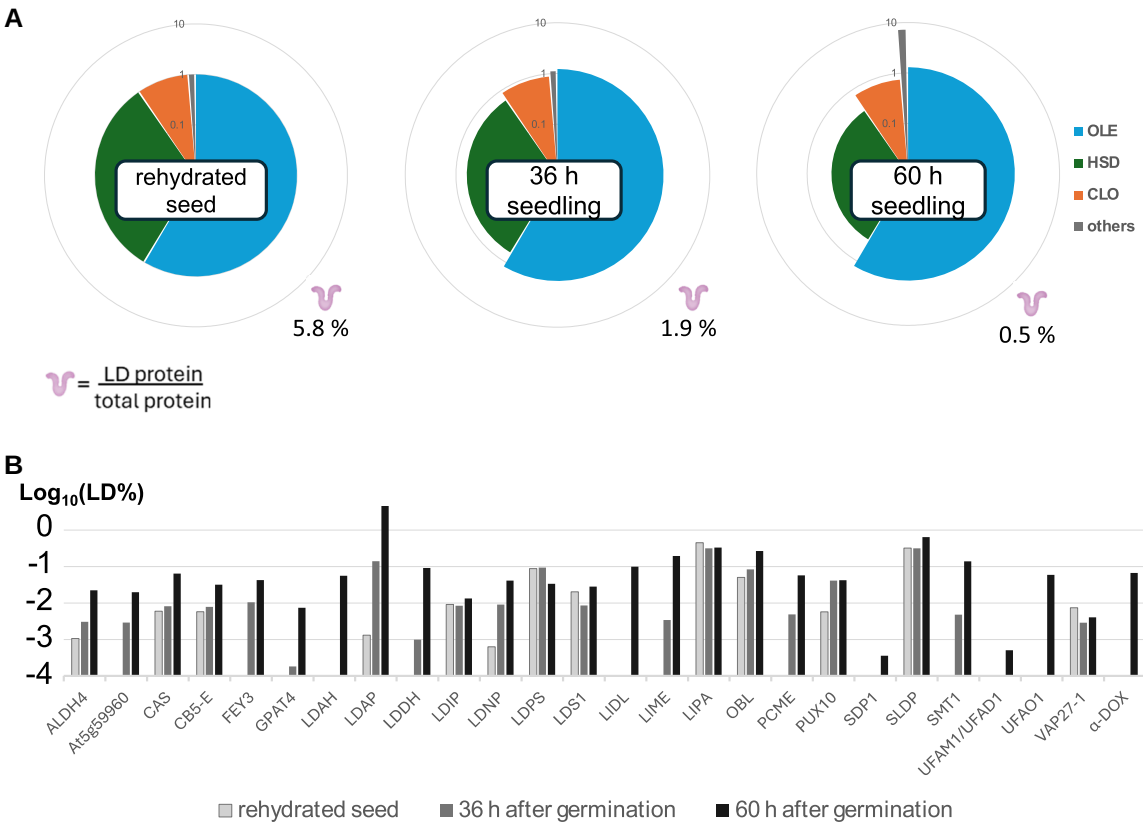

Fig. 2. The lipid droplet (LD) proteome strongly changes during seedling establishment in Arabidopsis. Relative abundances [molar ratios of proteins as a percentage based on relative intensity-based absolute quantification (riBAQ)] of LD proteins of LD enriched fractions of Arabidopsis seeds and seedlings are shown. (A) Radar plots of the developing LD proteome over the course of 60 h. The angle of the underlying pie chart represents the seed level and the radius shows the fold change from rehydrated seeds to the respective time point. Furthermore, the proportion of all % LD proteins in the total cellular proteome are displayed. (B) Low-abundance proteins shown in a bar chart. The absence of bars indicates protein families that were not detected in the sample. Abbreviations: ALDH4, aldehyde dehydrogenase; α-DOX1, α-dioxygenase; CAS, cycloartenol synthase; CB5-E, cytochrome b_5 isoform; CLO, caleosin; FEY3, FOREVER YOUNG 3; GPAT4, glycerol-3-phosphate 2-*O*-acyltransferase; HSD, hydroxysteroid dehydrogenases, steroleosin; LDAH, lipid droplet associated hydrolase; LDAP, LD associated protein; LDDH, LD dehydrogenase; LDIP, LDAP interacting protein; LDNP, LD-localized NTF2 family protein; LDPS, LD protein of seeds; LDS1/RABC1, LIPID DROPLETS AND STOMATA 1; LIDL, LD lipase; LIME, LD methyltransferase; LIPA, LD plasma membrane adaptor; OBL, oil body lipase; OLE, oleosins; PCME, prenylcysteine methylesterase; PUX10, plant UBX domain-containing protein; SDP1, sugar dependent 1-type TAG lipase; SLDP, seed LD protein; SMT1, sterol methyltransferase; UFAM1/UFAD1, unsaturated fatty acid methyltransferase/dehydrogenase; UFAO1, unsaturated fatty acid oxidase; VAP27-1, VAMP–associated protein. Proteomic data derives from Kretzschmar *et al.* (2018).

hypothesized to mediate protein–protein interactions via a predicted BTB/POZ domain (Kretzschmar *et al.*, 2020). Recently, Doner *et al* (2025) described the involvement of LDPS, together with oleosin, in the regulation of proper LD size during seed germination. They showed that the increase in LD size in *ole1* knockout mutants is reverted by additionally knocking out *LDPS*. Furthermore, LDPS interacts with OLE1 and OLE2 and was hypothesized to be involved in LD fusion leading to larger LD sizes.

As the seedling develops and switches to a photoautotrophic state, LDs cease to be essential as an immediate energy and carbon source. Concomitantly, the proteome of LDs transitions from that for a seed to a seedling (Fig. 2). This transition was followed up to 60 h after rehydration (Kretzschmar *et al.*, 2020). In this time course, most of the seed LD proteins are substantially reduced in total abundance from 5.7% to 0.5% of the total proteome (Fig. 2A). However, the relative composition of the four major LD proteins only changes to a minor degree, with the proportion of HSDs decreasing and LDAPs increasing (Fig. 2A). In contrast, the abundance of many of the minor LD proteins, which are, in most cases, not found in the seeds, sharply increases (Fig. 2B). One pertinent example of this increase is the LD-ASSOCIATED HYDROLASE 1 and 2 (LDAH1 and 2). While their functions in Arabidopsis are not yet clear, a homolog in the plant lesquerella (*Physaria fendleri*) called TAG lipase like-1 has been described as a TAG lipase involved in TAG remodeling, via the incorporation of hydroxylated fatty acids into TAG (Parchuri *et al.*, 2024). Likewise, LDAH1 and 2 might remodel and/or selectively degrade TAG during seed germination in Arabidopsis. Another family of Arabidopsis LD-bound lipases, referred to as OIL BODY LIPASE (OBL) 1 to 5, also shows differential

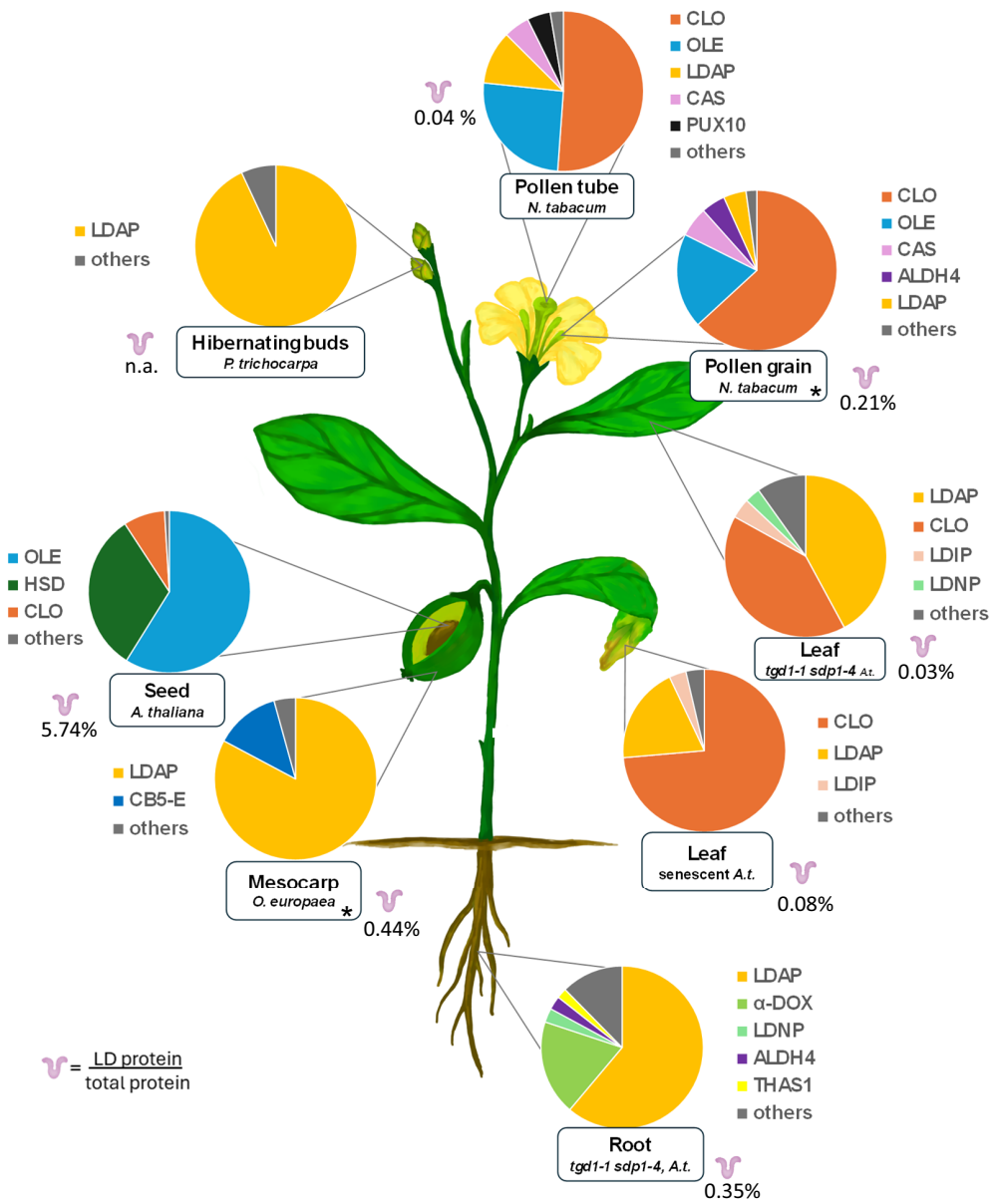

Fig. 3. Land plant organs carry highly specialized lipid droplet (LD) proteomes. Chimeric plant showing the relative LD proteomes [molar ratios of proteins as a percentage based on relative intensity-based absolute quantification (riBAQ)] of different plant tissues. Asterisks indicate that the underlying datasets were not obtained from LD-enriched but rather total cellular fractions. The proportion of all % LD proteins in the total cellular proteome are displayed. For *Populus trichocarpa*, no data on total cellular extracts were available in the dataset. Abbreviations: ALDH4, adehyde dehydrogenase; α-DOX1, α-dioxygenase; CAS, cycloartenol synthase; CB5-E, cytochrome b_5 isoform; CLO, caleosin; HSD, hydroxysteroid dehydrogenases, steroleosin; LDAP, LD associated protein; LDIP, LDAP interacting protein; LDNP, LD-localized NTF2 family protein; OLE, oleosins; PUX10, plant UBX domain-containing protein; THAS1, thalianol synthase. Proteomic data derives from Brocard *et al*. (2017), Ischebeck *et al*. (2014), Karagiannis *et al*. (2021), Kretzschmar *et al*. (2018, 2020), Scholz *et al*. (2024, 2026), and Veerabagu *et al*. (2021).

abundance between seeds and seedlings. OBL1 is found in dry seeds and is then quickly degraded while abundance of OBL3 is increasing (Kretzschmar *et al*., 2020) (Fig. 2B). While the role of these lipases is unknown, a homolog in tomato was found to be involved in the synthesis of oxylipin-derived volatiles (Garbowicz *et al*., 2018).

The breakdown of LD proteins required for the dramatic change in LD protein composition during the transition from seed to seedling is, in part, facilitated by the scaffold protein PLANT UBX DOMAIN-CONTAINING PROTEIN 10 (PUX10). PUX10 binds to LDs and recruits the AAA-type ATPase CELL DIVISION CYCLE 48 (CDC48), which acts

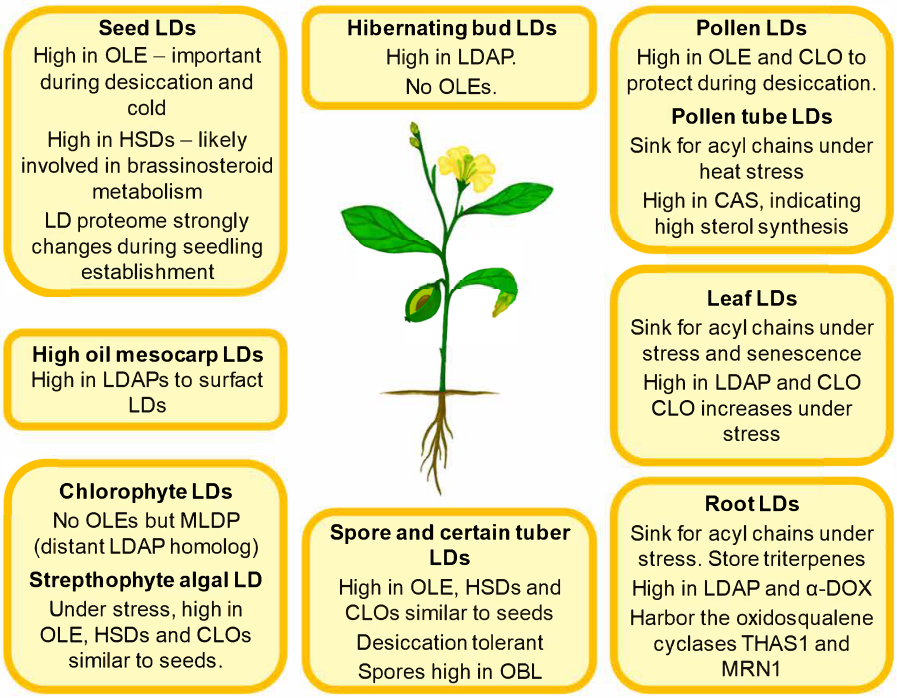

Fig. 4. Overview of the most relevant lipid droplet (LD) proteins and functions in different tissues. Schematic overview of a chimeric seed plant, spores, and freshwater algae focusing on the most relevant LD proteins and functions: in pollen grains (*Nicotiana tabacum*), leaves (*Arabidopsis thaliana*), mesocarp (*Olea europeae*), seeds (*A. thaliana*, *Coffea arabica*, *Chenopodium quinoa*, *Glycine max*, *N. tabacum*), hibernating buds (*Populus trichocarpa*), roots (*A. thaliana*), tubers (*Cyperus esculentus*), spores (*Physcomitrella patens*), and freshwater algae (*Chlamydomonas reinhardtii*, *Mesotaenium endlicherianum*). Abbreviations: α-DOX1, α-dioxygenase 1; CAS, cycloartenol synthase; CLO, caleosin; HSD, hydroxysteroid dehydrogenase, steroleosin; LDAP, LD associated protein; MLDP, major LD protein; MRN1, marneral synthase 1; OBL, oil body lipase; OLE, oleosin; THAS1, thalianol synthase 1.

as an unfoldase during protein degradation (Deruyffelaere *et al.*, 2018; Kretzschmar *et al.*, 2018). *pux10* mutant lines displayed a slower degradation of oleosins and HSDs. Recent evidence has also suggested a more general role for PUX10 (Li and Jarvis, 2024) since, in addition to LDs, it also localizes to the outer chloroplast membrane in Arabidopsis protoplasts and leaf tissue (Li and Jarvis, 2024).

Overall, the contribution of proteins with (putative) enzymatic or other cell biological functions to the LD proteome increases during seedling germination, while the structural oleosins are correspondingly degraded (Kretzschmar *et al.*, 2020). This supports the idea that LD function changes during seedling establishment, shifting from its storage role in seeds towards different roles in the developing plant, such as lipid remodeling and the production of volatiles.

Lipid droplet proteome diversity across different tissues

Apart from seeds, there is another important desiccation-tolerant structure in many plant species: pollen grains, which have evolved to spread the genetic material through unfavorable conditions. In regards to LDs in pollen, they have been best studied in Arabidopsis and tobacco, wherein they contain fewer LDs than seeds but more than in (unstressed) vegetative tissues (Rotsch *et al.*, 2017; Li *et al.*, 2022).

While proteomics data for LDs isolated from pollen in Arabidopsis are lacking; a total proteome analysis of mature pollen from Arabidopsis showed the presence of oleosins, a caleosin, and an LDAP (Grobei *et al.*, 2009). Transcript data support these findings (Honys and Twell, 2004). Interestingly, in both the proteomics and transcriptomics studies, the dominant oleosin and caleosin isoforms are OLE7 and OLE8, and CALEOSIN4 and CALEOSIN8, respectively, which are not of high abundance in seeds. This indicates that members of certain LD protein families diversified through evolution in regard to their tissue specificity.

For tobacco pollen LDs, considerably more proteomics data are available (Fig. 3). Total extracts of different development stages show that oleosins accumulate prior to desiccation but are degraded during pollen tube growth (Ischebeck *et al.*, 2014). LDAP levels, on the other hand, are higher during pollen development in the binuclear pollen stage (i.e. 56% of all LD proteins), when LDs accumulate (Ischebeck *et al.*, 2014), but lower in comparison in mature pollen (i.e. 5% of all LD proteins). Caleosins are found also in all tobacco pollen stages with higher abundance in the later stages, but no HSDs are

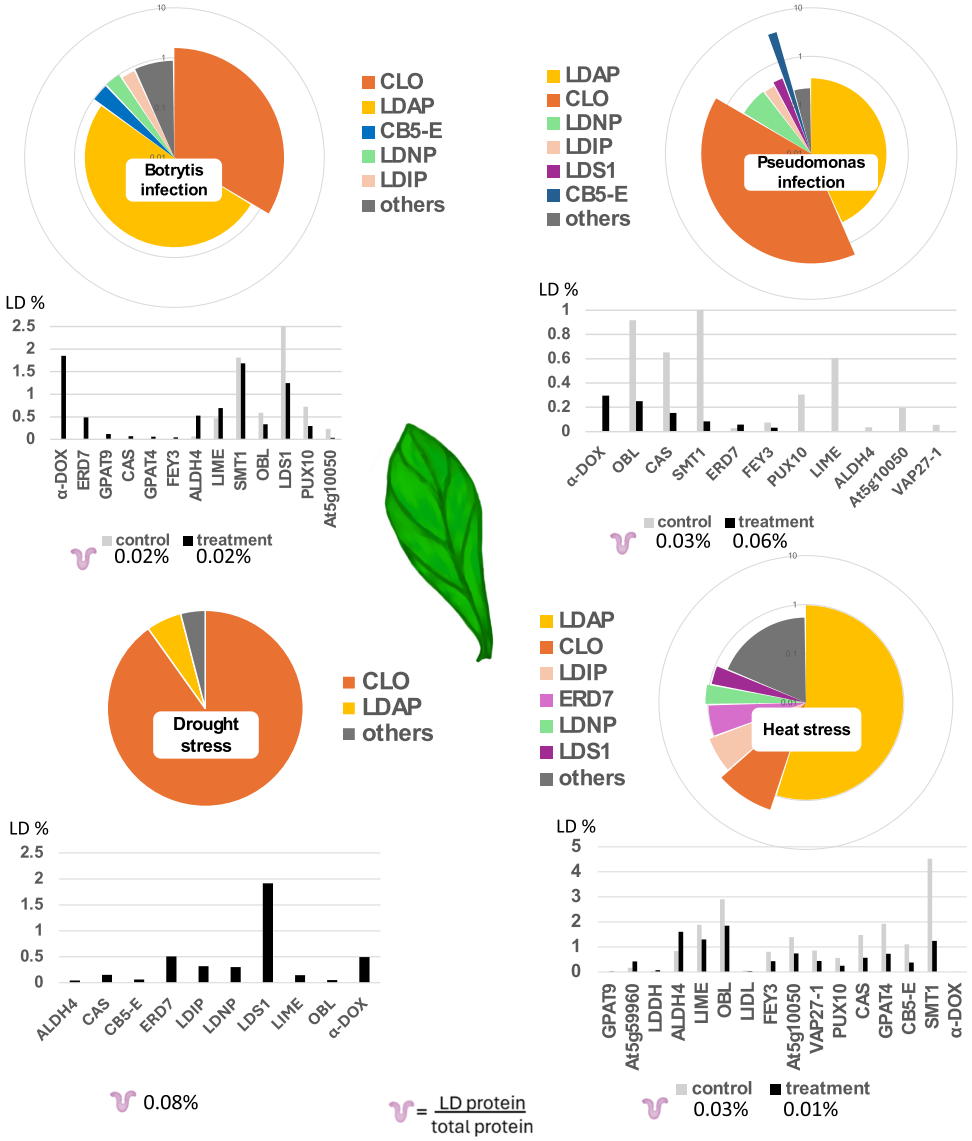

Fig. 5. The Arabidopsis leaf lipid droplet (LD) proteome dynamically changes under stress. Relative abundances [molar ratios of proteins as a percentage based on relative intensity-based absolute quantification (riBAQ)] of LD proteins of LD enriched fractions of stressed Arabidopsis leaves are shown. Pie charts (drought stress) and radar plots (*Pseudomonas syringae* and *Botrytis cinerea* infection, and heat stress) represent the most abundant LD proteins. If a control treatment was available, the radius represents the fold change from the control (represented by the angles in the underlying pie chart). The bar plots show the lower abundance proteins sorted by fold change from most induction on the left to most depletion on the right (drought stress is sorted alphabetically). Except for drought stress, all experiments were performed with the *tgd1-1 sdp1-4* double mutant. Abbreviations: ALDH4, aldehyde dehydrogenase; α-DOX1, α-dioxygenase; CAS, cycloartenol synthase; CB5-E, cytochrome b_5 isoform; CLO, caleosin; ERD7, EARLY RESPONSIVE TO DEHYDRATION 7; FEY3, FOREVER YOUNG 3; GPAT4, glycerol-3-phosphate 2-*O*-acyltransferase; GPAT9, glycerol-3-phosphate 1-*O*-acyltransferase; LDAP, LD associated protein; LDDH, LD dehydrogenase; LDIP, LDAP interacting protein; LDNP, LD-localized NTF2 family protein; LDS1/RABC1, LIPID DROPLETS AND STOMATA 1; LIDL, LD lipase; LIME, LD methyltransferase; OBL, oil body lipase; PUX10, plant UBX domain-containing protein; SMT1, sterol methyltransferase; VAP27-1, VAMP-associated protein. Proteomic data derives from Doner *et al*. (2021) and Scholz *et al*. (2024).

detected (Supplemental Data S1) (Ischebeck *et al*., 2014). As tobacco pollen tubes can be cultivated in larger amounts, LDs were successfully isolated from this tissue giving deeper insights to the pollen tube LD proteome. Similar to mature pollen grains, the proteins in LDs in pollen tubes consist predominately of caleosins, oleosins, and LDAPs (Kretzschmar *et al*., 2018) (Figs 3, 4). Among the lower abundance LD proteins, the amount of CYCLOARTENOL SYNTHASE 1 (CAS1) is conspicuously higher compared with other tissues (Supplementary Dataset S1). This protein is a member of the family of oxidosqualene cyclases and catalyses the formation of cycloartenol, the first committed step in

the biosynthesis of sterols (Corey *et al.*, 1993). The comparable high abundance of CAS1 in pollen tubes therefore likely underscores the importance of membrane lipid synthesis in pollen tube growth (Fig. 4).

Similar to pollen, roots have not been in the focus of classical LD research. However, recently, the *tgd1-1 sdp1-4* double mutant was employed in studies aimed at deciphering the root LD proteome in Arabidopsis (Scholz *et al.*, 2026). Herein, the LDAP protein family is the most abundant root LD protein (Figs 3, 4). Conversely, seed-specific LD proteins, like oleosin or steroleosin family proteins, are only found in relatively low amounts. CALEOSIN family proteins are also present in root LDs but at a low level, consisting of ∼1%.

Among the less abundant LD proteins of roots, LD METHYLTRANSFERASE 1 (LIME1), UNSATURATED FATTY ACID OXIDASE 1 (UFAO1), and UNSATURATED FATTY ACID METHYLTRANSFERASE/DEHYDROGENASE 1 (UFAM1/UFAD1) were found significantly enriched in the LD fraction (Scholz *et al.*, 2026). All three proteins were also confirmed to be localized to LDs via fluorescent protein-tagging and microscopy-based studies with either transiently transformed *N. benthamiana* leaves or *N. tabacum* pollen tubes. Further, based on their homology to proteins from the photosynthetic purple bacterium *Cereibacter sphaeroides*, LIME1, UFAO1, and UFAM1/UFAD1 are hypothesized to mediate the formation of furan fatty acids, similar to a pathway described in bacteria (Lemke *et al.*, 2020). Additionally, 14 other proteins were described to be LD associated in roots based on recent proteomics analyses (Scholz *et al.*, 2026). Among these are the oxidosqualene cyclases (OSCs) THALIANOL SYNTHASE and MARNERAL SYNTHASE, which are responsible for the synthesis of two different triterpenes (Fazio *et al.*, 2004; Xiong *et al.*, 2006) and localized to LDs in plant transient expression systems. OSCs catalyse different cyclisation reactions from (*S*)-2,3-oxidosqualene yielding cycloartenol, thalianol, or marneral (Field and Osbourn, 2008; Huang *et al.*, 2019). Their substrate and its precursor are hydrophobic molecules and could thus be stored in the LD's hydrophobic core. Indeed, squalene was found enriched in isolated LDs from roots, as were the immediate products of the OSCs and their esterified versions (Scholz *et al.*, 2026). While the free amphipathic triterpenes might reside in the LD monolayer, their hydrophobic esters are likely found in the LD core. As such, root LDs might be a key hub for synthesis and storage of hydrophobic secondary metabolites. Interestingly neither OSCs (i.e. THALIANOL SYNTHASE and MARNERAL SYNTHASE) were found in any other LD proteomic dataset from Arabidopsis (Supplementary Data S1). This is consistent with a transcriptomic atlas on Arabidopsis development (Klepikova *et al.*, 2016), where the respective transcripts were only detected in roots, reinforcing the notion that root LDs possess unique functionalities in Arabidopsis.

Finally, it is worthwhile mentioning that the abundance of α-DIOXYGENASE 1 (α-DOX1) in Arabidopsis root LDs (based on our proteomics dataset; Scholz *et al.*, 2026), is much higher than in other tissues (Figs 3, 4). α-DOX1 was initially described and characterized as a LD protein in leaves (Shimada *et al.*, 2014) where, as is discussed in more detail below, it is less abundant (Brocard *et al.*, 2017; Scholz *et al.*, 2024). Hence, the increased α-DOX1 protein amounts in roots might be due to the root culturing conditions used. Nevertheless, the potential root-specific function of α-DOX1 is an interesting topic for future studies.

Plasticity of leaf lipid droplets during senescence and in response to stress

Compared with roots, considerably more knowledge has been gathered with regards to the LD proteome in Arabidopsis leaves (Bouchnak *et al.*, 2023). However, the low abundance of LDs in wild type leaves has prevented the characterization of the native leaf LD proteome under regular growth conditions. Nevertheless, it is commonly observed that LDs accumulate in stressed or senescing leaves (Gidda *et al.*, 2016; Brocard *et al.*, 2017; Fernández-Santos *et al.*, 2020; Coulon *et al.*, 2024). Senescing leaves, for instance, show increased gene expression of *LDAP1* and *CLO3* (Brocard *et al.*, 2017) whose protein products are associated with the formation of LDs (LDAP, Pyc *et al.*, 2021) and the production of oxidized acyl chains (CLO3, Blée *et al.*, 2014; Shimada *et al.*, 2014), respectively. Interestingly, LDs in senescing leaves have been observed to be in close proximity to plastids and overexpression of *LDAP1* led to an accumulation of 18:3 acyl chains in TAGs of senescent leaves. Based on these observations, it was proposed that LDs in senescent leaves accumulate as lipid metabolites that are recycled from the plastid membranes (Brocard *et al.*, 2017; Coulon *et al.*, 2024). In contrast, stress-induced leaf LDs have been implicated to function in acyl chain remodeling of membrane phospholipids caused by different stressors, with the LDs serving as temporary sinks (Scholz *et al.*, 2024).

In terms of LD-based proteomic analyses, the LD protein compositions have been characterized for senescent (Brocard *et al.*, 2017) and drought-stressed leaves (Doner *et al.*, 2021). The LD proteomes of *tgd1-1 sdp1-4* double mutant plants subjected to heat stress or infected with either *Pseudomonas syringae* or *Botrytis cinerea* have been also characterized (Scholz *et al.*, 2024), and in doing so researchers have exploited the accumulation of LDs in vegetative tissues in this mutant (Fan *et al.*, 2014; Scholz *et al.*, 2024).

Across all leaf studies, the abundance of LD proteins in the total cellular fractions is much lower than in seeds (Figs 3, 5), although, through the enrichment of LDs, many known and novel LD proteins have been detected (Supplementary Dataset S1). For instance, similar to roots, proteins of the LDAP family are abundant in leaf LDs (Scholz *et al.*, 2026)

and conversely no oleosins are found (Figs 3–5). CLO3, on the other hand, is much more abundant in leaf LDs than caleosins are in LDs in other tissues. CLO3 has been postulated to be involved in oxylipin signaling due to its capacity to oxidize unsaturated fatty acids to generate epoxy fatty acids (Blée *et al.*, 2014; Rahman *et al.*, 2018). Furthermore, CLO3 is proposed to be involved in responses to salt, cold, and drought stress (Partridge and Murphy, 2009; Aubert *et al.*, 2010; Blée *et al.*, 2014). Compared with the LD proteome in developing seedlings (see also above, Kretzschmar *et al.*, 2020) it is notable that many changes in LD protein abundance from seeds to seedlings are accentuated in the mature leaf tissues. For example, among the OBL protein family, only the OBL3 isoform is detected in the leaf LD proteome (Scholz *et al.*, 2024), which is consistent with its increase in abundance in seedling development (Kretzschmar *et al.*, 2020).

Another study of LDs in Arabidopsis senescing leaves (Brocard *et al.*, 2017) focused primarily on CLO, LDAP, and LDIP family proteins, which were noted as all being enriched. We, therefore, reanalysed these published data to assess the abundance of all LD proteins that have been described so far (Fig. 3; Supplementary Dataset S1). As senescent leaves were not compared with non-senescent leaves in the former study (Brocard *et al.*, 2017), it is not easy to estimate which of the abundant proteins are up-regulated by senescence. However, in comparison with non-stressed control lines in the *tgd1-1 sdp1-4* double mutant background, CLO3 levels were elevated (Fig. 3). This is consistent with the increase in transcript levels of *CLO3* during senescence (Schmid *et al.*, 2005). Another notable difference is that GLYCEROL-3-PHOSPHATE ACYLTRANSFERASE 9 (GPAT), while at low levels in senescing leaf, was more abundant than in other (non-senescent) leaf samples. GPAT9 catalyses the addition of a first acyl chain to glycerol-3-phosphate to form lysophosphatidic acid as a first step of the Kennedy pathway (Shockey *et al.*, 2016; Singer *et al.*, 2016). Subsequent reactions form phosphatidic acid, a membrane lipid and precursor for other membrane lipids and TAG (Li-Beisson *et al.*, 2013). Thus, GPAT9 could be enriched in LDs in senescing leaves in order to channel acyl chains derived from senescence-induced thylakoid degradation into TAG synthesis. However, GPAT9 has been also reported to be localized to the endoplasmic reticulum (Gidda *et al.*, 2009), as are the subsequent reactions involved in TAG synthesis, even though other studies also raised the possibility of TAG synthesis at LDs (Roughan and Slack, 1982; Gidda *et al.*, 2009). While, it has yet to be determined if Arabidopsis GPAT9 is enzymatically active at LDs, another possibility is that the enzyme only resides there in an inactive form and transits to the endoplasmic reticulum when activated.

In addition to developmental processes, leaves along with their LDs need to adjust to a plethora of environmental inputs, including stresses like temperature stress, drought, or biotic interactions (Fig. 5) (Doner *et al.*, 2021; Scholz *et al.*, 2024). In a study of the LD proteome of drought-stressed leaves, CLO3 protein levels were very high in comparison with other leaf-based studies, reinforcing the involvement of CLO3 in drought stress response (Doner *et al.*, 2021). Similarly, in the same study EARLY RESPONSIVE TO DEHYDRATION 7 (ERD7) was highlighted as being one of the more abundant LD proteins compared with other leaf LD proteomes (Supplementary Data S1). ERD7 protein amounts are known to increase after ABA treatment, as this phytohormone is strongly involved in drought response, but also after salt stress or cold treatment (Barajas-Lopez *et al.*, 2021). Under cold stress, ERD7 has been implicated to be involved in membrane remodeling, but a similar function in drought-stressed leaves has yet to be determined.

Multiple studies reported that heat stress leads to increased TAG levels in leaves as a short-term response (Mueller *et al.*, 2015; Higashi and Saito, 2019), and Scholz *et al.* (2024) used the *tgd1-1 sdp1-4* mutant to analyse how this relates to the leaf LD proteome. Notably, the experiments in this latter study were performed using a protein cross-linking agent during the LD isolation procedure, resulting in increased abundance of several low-abundant LD proteins, but making comparisons with other studies difficult. Despite the fact that TAG levels can increase in leaves significantly upon heat stress (Higashi *et al.*, 2015; Shiva *et al.*, 2020) (Fig. 5), the comparison of heat stressed and unstressed did not lead to any obvious changes in the LD proteome, with only the relative abundance of CLO3 slightly increasing during heat stress (Fig. 5).

Other, more dramatic changes in the leaf LD proteome were observed under biotic stress using the pathogenic bacterium *P. syringae* and the necrotrophic fungus *B. cinerea* (Scholz *et al.*, 2024). In both treatments, CLO3 is induced relative to the control upon stress and makes up to 53% and 74% of the LD proteome (Fig. 5). This is consistent with the publicly available transcriptomic data, where CLO3 is highly induced in response to various biotic stresses. In this biotic stress environment, the amount of the low-abundant LD protein α-DOX1 also increased from being undetectable in controls to 0.3% and 1.8% after *P. syringae* and *B. cinerea* treatment, respectively (Fig. 5). Shimada *et al.* (2014) suggested that CLO3 and α-DOX1 act together in the formation of 2-HOT, an antimicrobial compound, which fits to the observed increase in their abundance. This is in contrast to heat stress, where α-DOX1 protein abundance did not increase, indicating that, unlike CLO3, α-DOX1 is specifically important in biotic stress responses of leaves.

Lipid droplet proteome plasticity in the course of evolution

Cytosolic LDs are found not only in large amounts in seeds of seed plants, but also in certain cells and tissues of other eukaryotes. For instance, in the green lineage, LDs are found in high number in green algae under stress (Moellering and Benning,

2010; Huang *et al.*, 2013), as well as in pre-akinetes and zygospores of zygnematophyte algae (Permann *et al.*, 2023; Permann and Holzinger, 2024), and in the spores of mosses (Huang *et al.*, 2009) and ferns (Gemmrich, 1981). They also accumulate to a large extent in certain yeasts, such as *Yarrowia lipolytica* (Mlickova *et al.*, 2004), in conidia (asexual spores) of fungi (Bhadauria *et al.*, 2012), and in adipocytes and hepatocytes of animals (Walther and Farese, 2012). Overall, they are considered to be present in most, if not all, eukaryotic cells, at least in small numbers.

As LDs are ubiquitously present, the question arises whether the protein players involved in their formation at the endoplasmic reticulum are conserved across eukaryotes as well. In addition to the already mentioned SEIPIN proteins, their interactors VAP27-1 and LDIP [referred to as promethin or Lipid Droplet Assembly Factor 1 (LDAF1) in yeast and in mammals] are also conserved across eukaryotes (Eisenberg-Bord *et al.*, 2018; Chung *et al.*, 2019; Greer *et al.*, 2020). Furthermore, the interactors of LDIP, the LDAPs, which are also involved in LD formation in plants, have homologs outside seed plants (Horn *et al.*, 2013). While the LDAP protein sequence is less conserved than that for the other three mentioned proteins, there is good evidence that homologies extend to at least green algae (de Vries and Ischebeck, 2020). This suggests that the last common ancestor of Chloroplastida had a molecular chassis for LD formation that we find in different confirmations across the extant diversity of chlorophytes and streptophytes. For example, the MAJOR LD PROTEIN (MLDP) of *Chlamydomonas reinhardtii* appears to have deep sequence homology to the MLDP of *Klebsormidium nitens*, which in turn shares sequence patterns with the LDAPs of angiosperms (de Vries and Ischebeck, 2020). Furthermore, also the perilipins, which are the main LD 'coat' proteins of animals, display sequence similarities to the LDAP of plants and might be homologous (Pyc *et al.*, 2021).

Apart from these proteins involved in LD formation, many enzymes found on plant LDs have homologs in other eukaryotes. These include HSDs, which are found in all kingdoms (Li *et al.*, 2007), caleosins (Hanano *et al.*, 2015) and OBLs (Eastmond, 2004), which are found in fungi, and LIME1/FUFM, which has homologs in bacteria (Omata *et al.*, 2024). The substrates of these enzymes might have changed over time, leading to different substrates in different kingdoms.

In addition to the individual proteins, whole expression programs and thereby LD proteome compositions overall seem to be evolutionarily conserved. This results in co-occurrences of proteins within the same cell that, in vascular plants, are characteristic for certain tissues, e.g. the proteome of LDs of leaves differs from those of seeds. However, single-celled zygnematophytes combine proteins within one cell that in land plants are only found in certain cell types (Goldbecker and de Vries, 2025), exemplified by the *Mesotaenium endlicherianum* LD proteome (Dadras *et al.*, 2023). The question of which evolutionary history shaped the diversification into different tissue-specific LD proteomes remains open. Yet, the answer is likely tied to the upstream regulation of tissue-specific proteomes. As such, we would like to make the case for an illuminating example of a proteomic pattern that we call the 'seed program', as it is highly characteristic for seeds and was first described in these structures, but is also found across streptophytes.

The 'seed program'

Several theories for the unparalleled success and evolutionary emergence of land plants are tied to their reproduction and propagation (Bowman *et al.*, 2016). The evolution of the seed was likely one of the highly favorable traits that led to the radiation of seed plants and their dominance in life on land. However, non-seed plants can also produce persistent, potentially dispersible structures as part of their life cycle or upon stress, including spores of land plants (Vollmeister *et al.*, 2024) and zygospores (Permann *et al.*, 2023) and pre-akinetes of streptophyte algae (Pichrtova *et al.*, 2016). What all these structures have in common is that they are often highly resistant to desiccation and other stresses and that they contain storage compounds often in the form of LD-stored TAG (de Vries and Ischebeck, 2020). Furthermore, the LD protein composition is remarkably similar in species ranging from streptophyte algae (the closest relatives to land plants) to seed plants (Kretzschmar *et al.*, 2020; Dadras *et al.*, 2023).

While the proteomic data on streptophyte algae are generally sparse, there are allied transcript data available that allows an assessment of the expression of LD-bound proteins. From these data, it is clear that oleosin-coding genes are up-regulated in desiccated, old cultures of streptophyte algae, and when they tend to form akinetes (Rippin *et al.*, 2017; de Vries and Ischebeck, 2020). A similar up-regulation is observed when streptophyte algae are subjected to either drought stress (Rieseberg *et al.*, 2023) or osmotic stress induced by salt and mannitol (Zegers *et al.*, 2026). Similarly, caleosins and HSDs have been also reported to be up-regulated in both streptophyte studies (Rieseberg *et al.*, 2023; Zegers *et al.*, 2026), completing the core of the seed LD proteome.

The only LD proteomic dataset from streptophyte algae comes from *M. endlicherianum* (Dadras *et al.*, 2023) (Fig. 6). In this study, cells were subjected to nutrient deprivation and grown at high cell density, but were not explicitly under drought stress. Nevertheless, they formed larger LDs and their LD proteome was similar to seeds with regards to having high levels of oleosins, HSDs, caleosins, and LDAPs (Figs 4, 6). This suggests that these LD protein families already obtained a stress-related function before the evolution of land plants. Green algae likely have no oleosin-coding genes in their genomes (de Vries and Ischebeck, 2020). It can therefore be assumed that this important building block of the seed program evolved in a common ancestor of streptophyte algae.

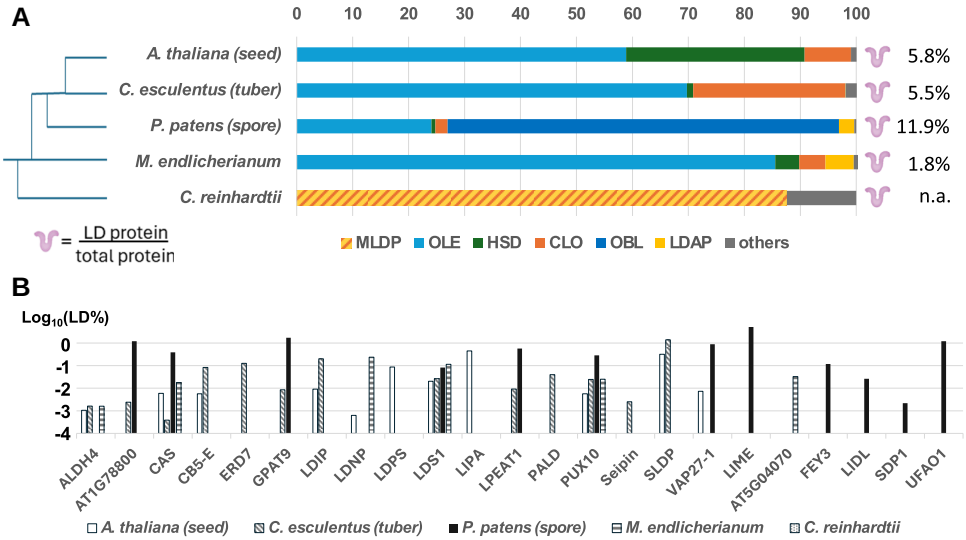

Fig. 6. The core seed lipid droplet (LD) proteome is conserved in streptophytes. Relative abundances [molar ratios of proteins as a percentage based on relative intensity-based absolute quantification (riBAQ)] of LD proteins of LD-enriched fractions of various oil-rich tissues of evolutionary distant species of the green lineage are displayed. Shown tissues are seeds (Arabidopsis), tubers (*Cyperus esculentus*), spores (*Physcomitrium patens*), and single cell algae (*Mesotaenium endlicherianum*, *Chlamydomonas reinhardtii*). (A) Schematic phylogeny depicting the relationship between the shown species. The most abundant proteins are shown as well as the relative LD protein content. For *Chlamydomonas reinhardtii*, no data on total extracts were available in the dataset. (B) Lower abundance proteins. The absence of bars indicates protein families that were not detected in the sample. Abbreviations: ALDH4, Aldehyde dehydrogenase; CAS, cycloartenol synthase; CB5-E, cytochrome b_5 isoform; CLO, caleosin; ERD7, EARLY RESPONSIVE TO DEHYDRATION 7; FEY3, FOREVER YOUNG 3; GPAT9, glycerol-3-phosphate 1-*O*-acyltransferase; HSD, hydroxysteroid dehydrogenases, steroleosin; LDAP, LD associated protein; LDIP, LDAP interacting protein; LDNP, LD-localized NTF2 family protein; LDPS, Lipid droplet protein of seeds; LDS1/RABC1, LIPID DROPLETS AND STOMATA 1; LIDL, LD lipase; LIME, LD methyltransferase; LIPA, LD plasma membrane adaptor; LPEAT1, lysophospholipid acyltransferase; MLDP, major LD protein; OBL, oil body lipase; OLE, oleosin; PALD, PROTEIN ASSOCIATED WITH LIPID DROPLETS; PUX10, plant UBX domain-containing protein; SDP1, sugar dependent 1-type TAG lipase; SEIPIN, Seipin; SLDP, seed LD protein; UFAO1, UNSATURATED FATTY ACID OXIDASE 1; VAP27-1, VAMP-ASSOCIATED PROTEIN 27-1 (Kretzschmar *et al.*, 2020; Niemeyer *et al.*, 2022; Dadras *et al.*, 2023; Hembach *et al.*, 2024; Torres-Romero *et al.*, 2024).

The seed program was then also used in early land plants, as it is found, for example, in the spores of *Physcomitrium patens*. Not only is the *P. patens* proteome closely related to that of seeds (Fig. 6A), their relative abundance of LD proteins is also similar (Hembach *et al.*, 2024). While LDs were not isolated, information is provided for the total cellular proteome of *P. patens* spores during germination and, for comparison, for protonema and gametophores. Overall, LD proteins make up 11.9% of the total proteome of spores with this value declining to 6.5% within 3 d of germination and being much lower in the vegetative tissues (<0.1%). The high level of LD proteins in spores is not surprising, as these appear (via electron microscopy) to be packed with LDs (Huang *et al.*, 2009), which likely fuels spore germination and the reconstitution of the photosynthetic apparatus. Apart from the four major LD proteins (i.e. oleosins, caleosins, LDAPs, and HSDs), which are dominated by oleosins, *P. patens* spores contain several OBL-type lipases with one of them being the overall most abundant protein. Further, during spore germination, the abundance of this OBL-type lipases decreases, and it is nearly absent in the vegetative growth stages of protonema and gametophore, indicating a pivotal role in the early phases of oil breakdown. This is different from Arabidopsis, where SUGAR DEPENDENT 1 (SDP1) is the lipase most important for TAG degradation (Eastmond, 2006), even though OBL1 is also present (Müller and Ischebeck, 2018). The genome of *P. patens* codes for four homologs of SDP1, but none were found in the available proteomic dataset (Hembach *et al.*, 2024) and their transcript levels are also relatively low overall (Fernandez-Pozo *et al.*, 2020). Interestingly, a putative cytosolic 13*S*-lipoxygenase (13S-LOX), PpLOX4, was found to be the second most abundant protein in *P. patens* spores, displaying a similar abundance pattern as the OBL1. This latter observation might explain the apparent lack of involvement of SDP1 in oil degradation and, thus, point towards a catabolic role of LOX in *P. patens*, similar to what has been hypothesized for LOX proteins in cucumber, sunflower, and barley seedlings, and olive pollen tubes (Feussner *et al.*, 1997, 2001; Matsui *et al.*, 1999; Zienkiewicz *et al.*, 2013). For instance, *P. patens* spores might utilize a 13S-LOX enzyme to first generate 13S-hydroperoxy fatty acids, which then are reduced to hydroxy fatty acids and released before being taken up into peroxisomes for β-oxidation. The cucumber 13S-LOX was described as LD associated in cotyledons (Feussner and Kindl,

1992; Hause *et al.*, 2000), as well as in cotyledons and pollen tubes of olive (Zienkiewicz *et al.*, 2013, 2014) and sunflower seeds (Yadav and Bhatla, 2011). Similarly, the main *P. patens* LOX could be associated with LDs and drive TAG breakdown in combination with the OBLs.

In seed plants, the 'seed program' occurs obviously mostly in seeds, and to some extent in pollen. However, in some species, it was probably also coopted in vegetative tissues that can undergo desiccation. For instance, LDs and oleosin transcripts are strongly increased in the leaves of the resurrection grass *Oropetium thomaeum* after desiccation (VanBuren *et al.*, 2017). Also, in the dicot *Lindernia brevidens*, another resurrection plant, oleosins and caleosins are up-regulated in leaves during desiccation (VanBuren *et al.*, 2018). Another example is yellow nutsedge (*Cyperus esculentus*). This grassy plant has evolved highly desiccation tolerant and oil rich tubers that sets it apart from its closest relative *C. rotundus* that forms starchy and non-desiccation tolerant tubers. These striking differences have evolved in a comparatively short time frame, as these two sister species had a common ancestor only 5.6 million years ago based on Bayesian molecular clock analysis (Niemeyer *et al.*, 2022). It is also notable that the tubers of yellow nutsedge have a similar LD proteome composition to seeds (Niemeyer *et al.*, 2022). For example, in the tuber LD proteome, oleosin and caleosin family proteins are mostly found, but so also are HSDs, as well as SLDP, which is seed specific in Arabidopsis (Kretzschmar *et al.*, 2020; Krawczyk *et al.*, 2022) (Fig. 6). This indicates that the reserve accumulation and desiccation tolerance are achieved by a seed-like expression program probably induced by distinct transcription factors (Niemeyer *et al.*, 2022).

Conclusions

LDs are ubiquitous organelles, yet their composition and functionality diversified strongly during evolution and across plant tissues. Initial research focused on LDs in seeds highlighted their importance as a lipid storage organelle, but more recent results in non-seed plants suggest that this 'seed program' is evolutionarily older and has developed as a strategy to persist in unfavorable environmental conditions. Seed-like LD proteins, such as oleosin homologs, can thus also be found in moss and streptophyte algae (Dadras *et al.*, 2023; Hembach *et al.*, 2024), as well as in specially adapted non-seed tissues (VanBuren *et al.*, 2017; Niemeyer *et al.*, 2022).

Based on studies in LD-rich tissues, a working model of LD formation in plants, which includes functional contributions by the SEIPIN, LDAP, and LDIP proteins, has been established (Taurino *et al.*, 2018; Greer *et al.*, 2020; Pyc *et al.*, 2021; see also review by Guzha *et al.*, 2023). Likewise, there is a considerable understanding of the processes underlying the mobilization of the stored lipids in LDs during germination and early seedling growth (Eastmond, 2006; Kelly *et al.*, 2011; Thazar-Poulot *et al.*, 2015). Indeed, by following the LD proteome during germination and seedling establishment important insights into the developmental plasticity of LDs during this stage of plant development have been obtained (Kretzschmar *et al.*, 2018, 2020). By contrast, the adaptability of LDs to stresses in vegetative plant tissues is less well known, and tissue-specific differences between LDs are just starting to be explored. Here, we surveyed our current knowledge on non-seed LD proteomes focusing on Arabidopsis, which has been the most widely used plant (model) species for LD proteomic studies. In doing so, leaf and root LDs are now known to be well distinct from seed LDs and not fulfilling the so-called 'seed program'—as evidenced by the absence of oleosins, the predominance of LDAPs, and the importance of different members of LD protein families like CLO3 instead of CLO1 and CLO2. These differences likely evolved to tailor LD function(s) to the tissue-specific needs, as well as the adaptability of the organelle's proteome in different tissues. The composition of leaf LDs is especially dynamic, underlining a more active role in the lipid homeostasis of leaves (Gidda *et al.*, 2016; Scholz *et al.*, 2024). LD research will need now to find or use additional ways to increase the number of LDs in plants, for example by overexpressing diacylglycerol acyltransferases (Vanhercke *et al.*, 2019). Alternatively, new methods could be developed to sufficiently enrich LD proteins from vegetative (unstressed) tissues with a low number of LDs. This exploratory work combined with a functional characterization of individual LD proteins will contribute to a global view on the subcellular and physiological function of LDs across species and tissues.

Next to the proteome, a characteristic difference between LDs isolated from different tissues is the types of hydrophobic compounds they store, including hydrophobic specialized metabolites such as terpenoids. While specialized metabolism has sprouted its own ramifications across the diverse lineages of streptophytes (Fernie *et al.*, 2024), we do not know how these are reflected in the diversity of LD metabolomes. Understanding how the different compounds are synthesized, packaged, and ultimately mobilized will pave the way for biotechnological approaches for the sustainable production of valuable hydrophobic compounds.

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Conflict of interest

The authors declare no conflicts of interest.

Supplementary data

The following supplementary data are available at *JXB* online.
Table S1. Proteomic datasets used in the meta-analysis.
Dataset S1. Proteomic data surveyed in this review.

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Data availability

Proteomics data were acquired from the indicated publications and have been uploaded to https://www.ebi.ac.uk/pride/ by the respective authors. Datasets used and their identifiers can be found in Supplementary Table S1.

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