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REVIEW ARTICLE

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# Transition dynamics in plastid interconversion in land plants

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**ABSTRACT**

In land plants, plastids acquired different functions and structures in parallel with the increasing genetic, developmental, and morphological diversity attained by the plant tissues. There are transition dynamics among the morpho-functional features of the different plastid types. This review is focused on plastid structure and interconversion with a focus on recent findings and a special attention to plastid types that are less known than chloroplasts. The morpho-physiological and biochemical differences, which explain the multiple functions of each plastid type and the transcriptional and post-translational modulation of plastid capabilities are here described. The structural dynamism of plastids is also discussed through their ability to produce protrusions called stromules and the activity of lipoprotein particles known as plastoglobules. As a consequence of the proteome differences among plastid types, the conversion from one type of plastid to another requires an organellar proteome reorganization with a turnover of plastid proteins, but also a differentially regulated import of nuclear-encoded proteins. Plastid degradation by macroautophagy and microautophagy pathways is also described. Taken together, all this information allows us to interpret plastids as sensors in development and plastid interconversion as a way that the plant uses to modify its growth.

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Chlorophagy; plastid interconversion; plastid types; plastoglobule; plastome; stromule

## Introduction

In land plants plastids are involved in many processes including photosynthetic $CO_2$ fixation, nitrogen and sulfur assimilation, amino acid, lipid and fatty acid (FA) synthesis, starch and oil storage, fruit and flower coloration, gravity sensing, stomatal functioning, environmental perception, and production of secondary metabolites (Solymosi and Keresztes 2013).

Plastids arose from polyphyletic endosymbiotic events during which at least two ancestral organisms, i.e. a photosynthetic prokaryote endosymbiont, usually a member of the β-cyanobacteria, and a heterotrophic, aerobic, proto-eukaryotic host, i.e. a single-celled ancestor of the Archaeplastida, including green, red and glaucophyte algae, and land plants (McGrath 2020). The two organisms became inextricably linked due to several processes occurring during their co-evolution (Ševčíková et al. 2015; Sibbald and Archibald 2020). These processes include gene transfer from the endosymbiont to the nucleus of the host and the occurrence of intense communication between the plastid DNA and the host nucleus, but also loss of some genes. As reviewed by McGrath (2020), plastids recruited for their functioning proteins encoded by the nucleus of the eukaryotic host, but also bacterial proteins of non-cyanobacterial origin. Secondary, tertiary, and higher order acquisitions of plastids occurred when, after the first endosymbiontic event, the eukaryotic cell with a "plastid" was engulfed by another eukaryote, which was then engulfed by another one, and so on. This type of subsequent phagocytosis events led to the acquisition of "complex" plastids. According to the endosymbiont-host coevolution, the most of present eukaryotes with plastids acquired them from red or green algae in the form of complex red or green plastids. For this reason, and as a consequence of gene transfer to the nucleus, land plants contain a mosaic of genetic material in their nuclear genomes coming from both red and green algae. This has led to the "shopping bag" model of plastid evolution. According to this model, of which "kleptoplasty", which will be described in a following paragraph, is an example supporting the model, genetic contributions from multiple endosymbionts over time contributed to the establishment of a permanent photosynthetic plastid.

In contrast with most algae, during the evolution of land plants, plastids became specialized and diversified in parallel with the increasing genetic, developmental, and morphological complexity and diversity acquired by the host organism, and its tissues. Plastid differentiation is concomitant to cellular differentiation and is controlled by genetic and environmental factors. Numerous studies on the regulatory pathways in plastids have focused on light-induced switching and phytohormonal treatments (Larkin 2014; Al-Babili and Bouwmeester 2015; Liu et al. 2017), and on the interaction between plastids and phytohormones in plant stress responses (Bittner et al. 2022).

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The shape of the plastid is flexible and, at least in part, governed by osmotic effects due to the hypo-osmotic surroundings of the organelle, and by the activity of mechano-sensitive ion channels of the plastid membranes (Jarvis and López-Juez 2013, 2014). In accordance, the term plastid, from the ancient Greek word "plastos", refers to the fact that the organelle can be easily shaped or molded, with this contributing to the adaptation of higher plants to the environment. There are transition dynamics among the functional and morphological features of the different plastid types, with most of them not showing a definitive specialization. However, in some cases, e.g. in gerontoplasts, the specialization becomes irreversible (Shah et al. 2016).

Most plastid proteins are encoded by nuclear genes and synthesized in the cytosol as precursor proteins. These proteins exhibit N-terminal transit peptides that govern import into the plastid stroma through the TOC (Translocon on the Outer Chloroplast membrane) – TIC (Translocon on the Inner Chlording toroplast membrane) translocases and that are removed by a stromal processing protease (Celedon and Cline 2013). The plastid retains a small genome from its cyanobacterial ancestor, containing about 90 protein-coding genes mainly related to photosynthesis, transcription, and translation (Christian et al. 2023). However, the plastids of higher plants still contain 2000–5000 unique proteins, and about 4–11% of the nuclear genome is plastid-targeted, with horizontal gene transfer from the plastid genome to the nuclear genome contributing to this situation. This transfer appears to have occurred rapidly after endosymbiosis and to have caused a strong interdependence between plastid genome (plastome) and nuclear genome (Christian et al. 2023).

Although plastid types are dynamically interconvertible, as shown in the first paragraph of the review, classification is usually based on their prevalent function. It generally reflects their predominant morphological traits defined by the nuclear-coded proteins according to a pathway, named *anterograde*, of plastid biogenesis and maintenance (Solymosi and Keresztes 2013). However, this classification is simplistic, and the nomenclature is often too rigid, needing to be refined to reflect the morpho-physiological and biochemical differences that justify the multiple functions of each plastid type and the modulation of plastid capabilities at both transcriptional and post-translational levels (Choi et al. 2021). In fact, in recent years, the combination of modern techniques and genetic analyses has expanded our current understanding of plastid morphological and functional diversity also showing a plastid-type specific signaling named *retrograde* organellar signaling (Teige et al. 2022; Sierra et al. 2023).

Altogether, and as also recently suggested (Mackenzie and Mullineaux 2022), recent findings suggest that specialization within plastid populations perfectly aligns with the different cellular properties.

## Aim

The present review is focused on plastid structure and interconversion with attention to plastid types less investigated than chloroplasts, considering recent findings, but also older literature deemed most significant in view of the recent results. Plastid transition dynamics are discussed, and it is shown that plastid interconversion is essential for successful plant development and for its modulation. Moreover, it occurs concomitantly with the developmental changes that characterize plant life. In the review, a particular attention is paid to the chromoplast, because it has been suggested to be the most recently evolved plastid type (Kuntz and Rolland 2012), and because the structural changes associated with its genesis involve a deep reorganization of the plastid protein content and a global reprogramming of nuclear gene expression and primary metabolism (Llorente et al. 2020). Attention is also paid to origin, dynamics and death of gerontoplasts, because they are at the end point of plastidial interconversion and have been rarely described in detail.

The general aim of the review is to show plastids as structures, which through their dynamism, represent an integral and essential part of plant development.

## Morpho-functional features of old and new plastid types

Based on their phenotype, plastids are classically divided into categories based on color, morphology, and ultrastructure (Figures 1 and 2) (Wise 2007). The non-photosynthetic plastids can be divided into leucoplasts, colorless plastids, and chromoplasts, plastids that exhibit red, orange, or yellow colors due to carotenoid accumulation, whereas chloroplasts are the photosynthetic plastids.

*Proplastids* are undifferentiated plastids present in meristematic cells, and sometimes in egg cells (Hagemann and Schröder 1989), tapetal cells and microspores (Figure 1(A)) (Pacini et al. 1992). Fewer than ten proplastids are contained per meristematic cell, each of which with about ten plastid DNA copies (Jarvis and López-Juez 2013, 2014). The plastid DNA transmission across generations in angiosperms normally occurs through the egg cytoplasm because the plastid DNA is degraded in pollen, but there are exceptions (Hagemann and Schröder 1989; Jarvis and López-Juez 2013, 2014).

In approximately 80% of angiosperms, plastids are inherited from the maternal parent, whereas other species transmit plastids biparentally. The maternal inheritance is a non-Mendelian inheritance due to plastid evolution as endosymbiont (Sakamoto and Takami 2023). It is explained by the segregation of maternal plastids after fertilization because the zygote is surrounded by the maternal cytoplasm. In contrast, the biparental inheritance shows plastid transmission from both parents. In some species, maternal inheritance is not absolute and paternal leakage occurs at a very low frequency (Sakamoto and Takami 2023). The theory of maternal dominance linked to plastid evolution as endosymbiont is based on the prediction that the plastid DNA needs to be strictly controlled by the host cell and that the only replication of the maternal genome is advantageous over zygotic hybridization to prevent organelle genome from self-evolving (Sakamoto and Takami 2023).

Proplastids possess only primordial internal membranes (Liang et al. 2018). In *Arabidopsis thaliana* (L.) Heynh.

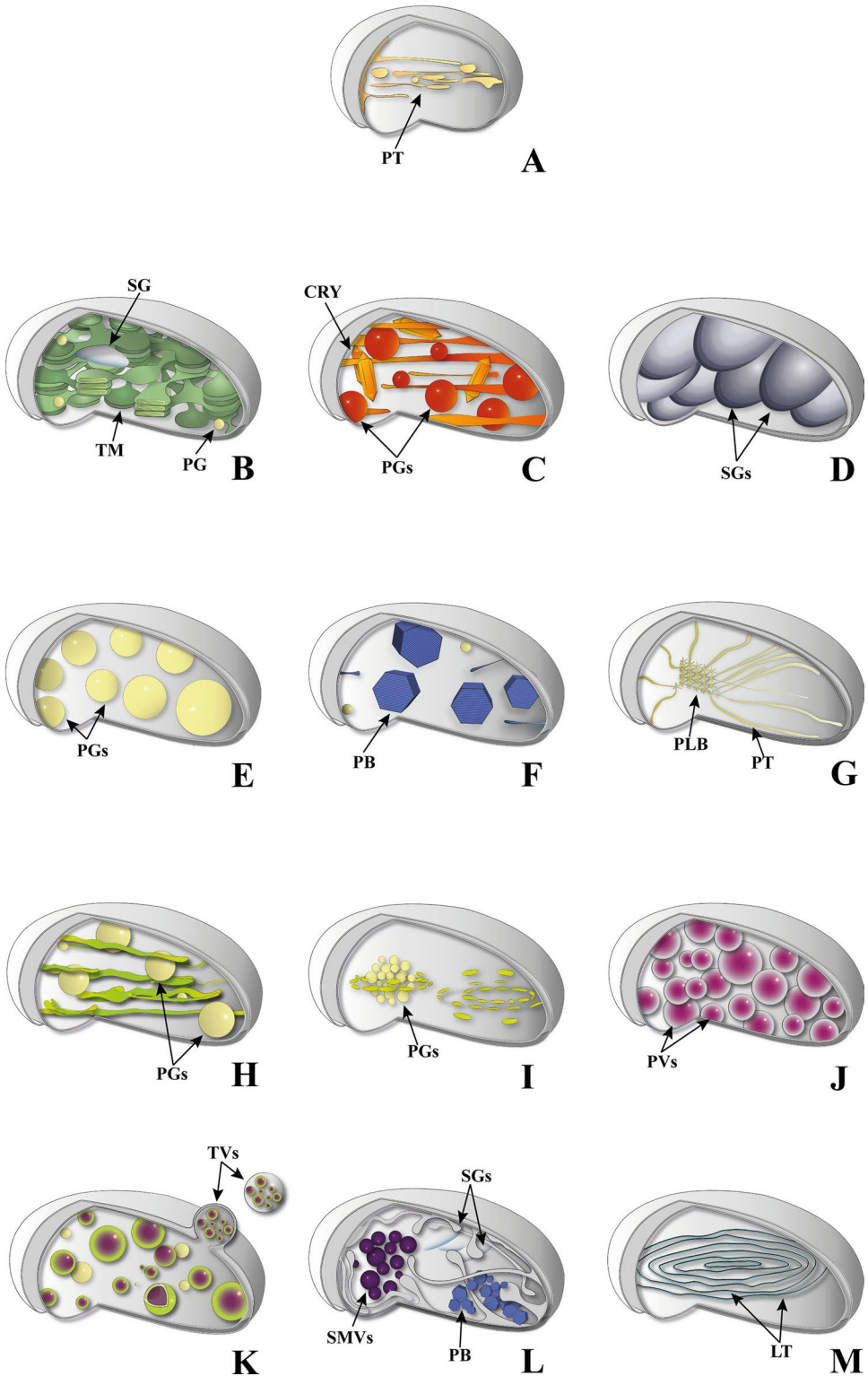


**Figure 1.** Schematic representation of the main types of plastids. (A) Proplastid; (B) chloroplast; (C) chromoplast; (D) amyloplast; (E) elaioplast; (F) proteinoplast; (G) etioplast; (H) gerontoplast; (I) desiccoplast; (J) phenyloplast; (K) tannosome; (L) xyloplast; (M) lamelloplast; CRY: crystal; LT: lamellar thylakoid; PB: protein body; PG: plastoglobule; PLB: prolamellar body; PT: prothylakoid; PV: phenol vesicle; SG: starch granule; SMV: secondary metabolites vesicle; TM: thylakoid membrane; TV: tannosome-forming vesicle.

cotyledons 24 h after germination, the membranes present in the proplastids are arranged as tubule-vesicular prothylakoids (PTs) (Figure 1(A)) with a wide lumen, no chlorophyll, but the presence of contact sites with the inner envelope membrane (Kowalewska et al. 2019). These contact sites are possibly involved in the entry of key proteins for the intra-plastid trafficking according to the TOC–TIC model (Celedon and Cline 2013).

There are at least two different functional forms of proplastids. The proplastids of the meristematic and embryonic tissues, as well as of the dedifferentiated (callus) cells, which are the precursors to all other plastid types, and proplastids

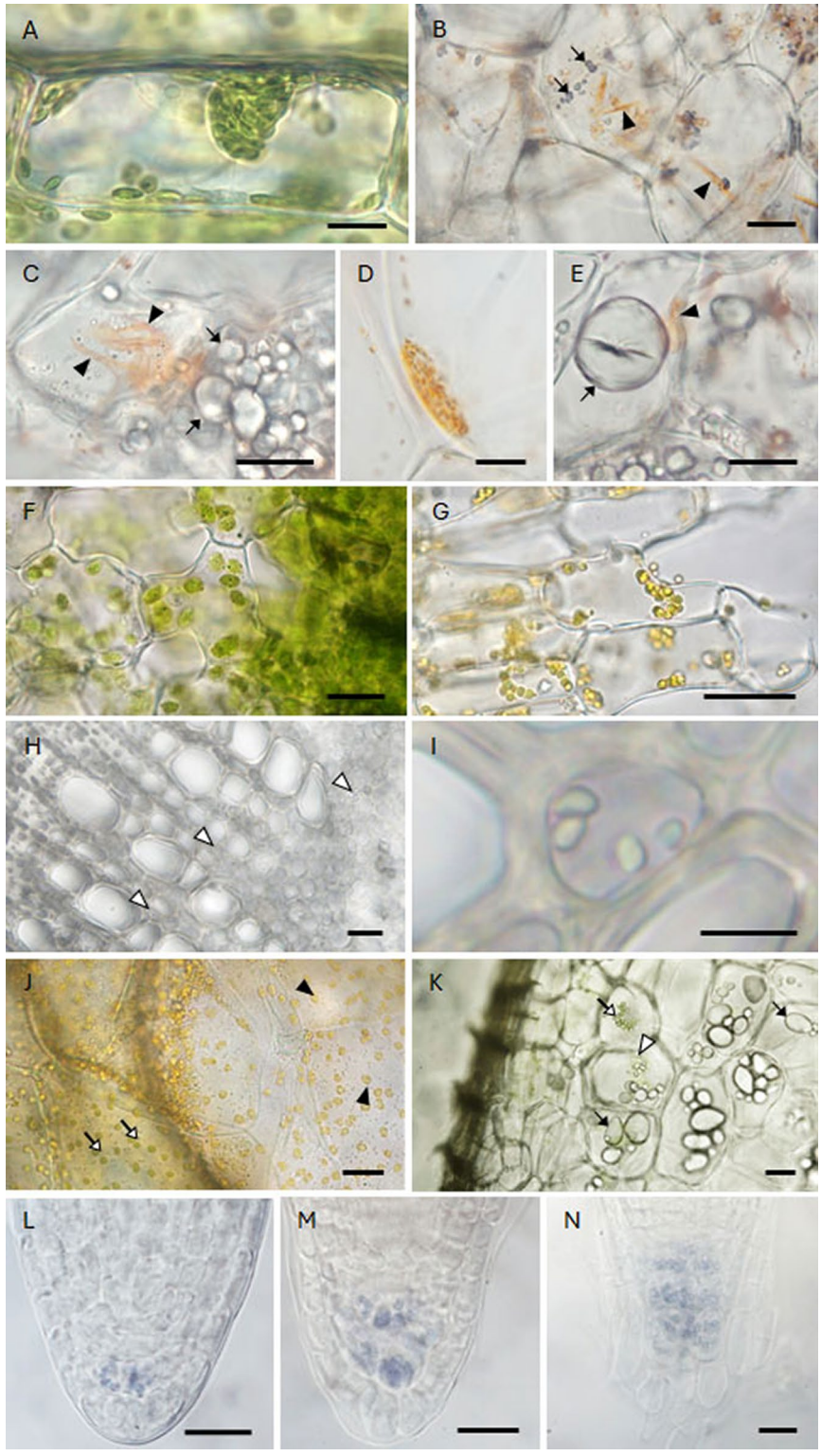


**Figure 2.** Different types of plant plastids observed under the light microscope. (A) Chloroplasts in a leaf chlorenchyma cell of *Elodea canadensis* michx., distributed around the vacuole. Due to cytoplasmic streaming activated by the microscope light, most chloroplasts appear locally grouped. (B) Crystal structures formed by carotenoid accumulation in phloem parenchyma cells of *Daucus carota* L. (arrowheads) hypocotyl. Small starch granules, stained with Lugol's reagent (arrows), are also visible in the same cells. (C) Membranous chromoplasts (arrowheads) in the parenchyma cells of an *Ipomoea batatas* (L.) lam. storage root. The cells also contain large starch granules (arrows). (D) Globular chromoplasts in a tomato (*Solanum lycopersicum* L.) mesocarp cell. (E) Storage starch in the form of a single large crystalline granule (arrow) within a parenchyma cell of an *Ipomoea batatas* (L.) lam. storage root. In the background (arrowhead) an accumulation of carotenoids is also visible. (F) Chloroplasts in spongy mesophyll cells of a *Ficus elastica* roxb. ex hornem. leaf. (G) Gerontoplasts in spongy mesophyll cells of a *Ficus elastica* roxb. ex hornem. leaf, resulting from chloroplast conversion by senescence. (H) Xyloplasts (arrowheads) in parenchyma cells of secondary xylem rays of *Eucaliptus robusta* Sm. leaf petiole. (I) Magnification of a parenchyma cell containing xyloplasts. (J) Chloroplasts (arrows) and chromoplasts (arrowheads) in pepper (*Capsicum annuum* L.) in confining mesocarp cells. (K) Large (black arrow) and small (arrowhead) amyloplasts in storage parenchyma cells of potato (*Solanum tuberosum* L.) tuber. The chloroplasts (white arrow) around the nucleus derive from greening under light of small amyloplasts. (L–N) Stages of differentiation of statocytes, containing statoliths, in the root calyptra of *Arabidopsis thaliana* (L.) heynh. Bars= 25 µm (A–H, J–K); 5 µm (I); 20 µm (L–N).

of root nodules located in proximity of symbiotic nitrogen-fixing bacteria, which are involved in incorporating atmospheric nitrogen into nitrogenous compounds (Solymosi and Keresztes 2013; Choi et al. 2021).

*Chloroplasts* are green in color and present in all photosynthetic tissues. They contain an internal system of thylakoid membranes associated with chlorophyll and carotenoid pigments, essential for the light reactions of photosynthesis (Figures 1(B) and 2(A,F)). These plastids are also essential for FAs and amino acids biosynthesis, and for the synthesis of porphyrins, isoprenoids, and secondary metabolites. However, only a small fraction of the enzymatic machinery involved is encoded in the chloroplast plastome (Sabater 2018).

*Chromoplasts* are yellow, orange or red. Synthesis and storage of high levels of carotenoid pigments occur in these plastids, which are naturally present in flowers and fruits, but also in roots after intensive breeding procedures (Rodriguez-Concepcion and Stange 2013). Chromoplasts serve to attract pollinators and seed dispersers or for the storage of hydrophobic metabolites in addition to carotenoids (Rottet et al. 2015).

During their development, the carotenoids form globular, round, coiled-shaped crystals stored in hydrophobic structures named plastoglobules (PGs) (Schweiggert et al. 2011) (Figures 1(C) and 2(B–E,J)). Plastoglobules are attached to thylakoids and function in lipid biosynthesis, storage and cleavage (Austin et al. 2006; Rottet et al. 2016).

Leucoplasts include amyloplasts, elaioplasts, etioplasts, proteinoplasts, in addition to proplastids.

Amyloplasts are the sites of starch storage and are found in roots, stems, cotyledons, seed endosperm, and tubers (Figures 1(D) and 2(B,C,E,K)). Amyloplasts are also involved in the gravity response in roots and shoots (Nakamura et al. 2019) (Figure 2(L–N)). During the amyloplast membrane formation, free FAs, lysophospholipids, lysophosphatidylcholine, lysophosphatidylethanolamine are also accumulated into the starch granules (Gayral et al. 2019). Unlike other plastid types, amyloplasts often coexist with other plastid types within the same cell (Figure 2(B,C,E,K)). Moreover, in the tissues of species such as *Cucurbita moschata* Duchesne, *Bactris gasipaes* Kunth, and *Ipomea batatas* (L.) Lam. plastids known as amylochromoplasts, able to store starch granules with carotenoid crystals simultaneously, have been observed (Jeffery et al. 2012; Hempel et al. 2014; Zhang et al. 2014).

Elaioplasts, also called oleoplasts, are plastids specialized for lipid and terpenoid synthesis (Figure 1(E)), e.g. in oil seed species, and are important for exine formation during pollen development from tapetal cells (Quilichini et al. 2014). Elaioplasts may be exported into secretory pockets with a role in conferring the aroma and taste of various fruits, such as kumquat [*Fortunella margarita* (Lour.) Swingle] fruits (Zhu et al. 2018).

The proteinoplasts, also called proteoplasts or aleuroplasts, seem to have a role in protein storage as protein bodies (PBs) (Figure 1(F)) and for this reason are present in many different cell types (Lopez-Juez and Pyke 2005).

Etioplasts develop in plants grown under continuous darkness, and rapidly change into chloroplasts upon illumination. During leaf development, under dark conditions proplastids differentiate into etioplasts, under light conditions into chloroplasts (Kowalewska et al. 2016).

The most important features of etioplasts are the absence of chlorophyll and the presence of an internal network of paracrystalline membranes known as the prolamellar body (PLB) (Figure 1(G)). In general, a single well-arranged PLB is present, but also tubular prothylakoids (PTs) are formed. These structures are interspersed with PGs containing high amounts of carotenoids, mainly lutein and violaxanthin (Choi et al. 2021) (Figure 1(G)). Differently, the etio-chloroplasts contain chlorophylls and possess small PLBs, often found in multiple interconnections with chloroplast-like thylakoids.

Etio-chloroplasts are considered a transition stage to chloroplasts (Solymosi and Schoefs 2010) and are present in angiosperms, gymnosperms and ferns.

Gerontoplasts are the senescent forms of chloroplasts but are also observed under stress conditions (Biswal et al. 2012). When the senescence process starts, these plastids undergo changes in ultrastructure which are difficult to define at least up to the degradation of their nucleic acid (Dyer and Osborne 1971). However, some features are specific to the gerontoplasts. They do not contain starch granules at maturity, their thylakoids and chlorophylls are degraded, PGs are enlarged and in high number (Biswal et al. 2012) (Figures 1(H) and 2(G)).

Desiccoplasts, also known as xeroplasts, are specialized plastids of desiccation-tolerant plants, in which they can be interconverted between chloroplasts and proplastids (Solymosi et al. 2013; Solymosi and Keresztes 2013). They resemble small chromoplasts containing several large PGs and only few thylakoids arranged often in concentric vesicle layers (Figure 1(I)). They are formed by a dedifferentiation process in the cells of dehydrated leaves of these specialized plants. During dehydration, the thylakoid system of the leaf chloroplasts is dismantled, and chlorophylls and carotenoids are degraded. Upon re-hydration, the desiccoplasts are transformed into functionally active chloroplasts (Solymosi and Keresztes 2013).

Phenyloplasts, another particular plastid type, are colorful plastids enriched in phenols (Figure 1(J)) (Brillouet et al. 2014). These plastids derive from chloroplasts and are formed to ensure phenylglucoside cell homeostasis. Their formation has been described in *Vanilla planifolia* Jackson ex Andrews fruit and starts with the generation of loculi between the thylakoids and phenol vesicles (PVs) (Figure 1(J)). The loculi are progressively filled with phenol glucosides, which accumulate as solid amorphous deposits up to the end of the maturation of the organelle (Brillouet et al. 2014).

Tannosomes are chloroplast-derived structures where polymerization of tannins occurs. They are formed through the pearling of unstacked thylakoids into 30 nm spheres which then migrate into the vacuole within vesicles (tannosome vesicles, TVs, Figure 1(K)). The vesicles originate from the chloroplast and are enveloped by a membrane composed of both chloroplast delimiting membranes (Figure 1(K)). The polymerization of the tannins occurs within the tannosome (Brillouet et al. 2013).

Xyloplasts are plastids observed during secondary vascular tissue differentiation (Figure 2(H–L)). Xyloplasts arise from proplastids, or more frequently, from amyloplasts, and participate in the synthesis of monolignol precursors (Pinard and Mizrachi 2018) and may contain also starch granules (SGs), secondary metabolite vesicles (SMVs) and protein bodies (PBs), as exemplified in Figure 1(L). The analysis of their type and function has been carried out in *Populus trichocarpa* Torr. & Gray, *Populus tremula* L. and *Eucalyptus grandis* W.Hill, where it has been demonstrated to be affected by the diversity of cell types present in wood and by the developmental changes associated with xylogenesis (Pinard et al. 2019).

Iridoplasts are specialized plastids present in the adaxial epidermal cells of the iridescent leaves of species such as *Begonia pavonina* Ridl., *Phyllagathis rotundifolia* Bl., *Trichomanes elegans* L.C.Rich., and *Selaginella erythropus* (Mart.) Spring. They are observed in the leaves of plants grown under the canopy of densely populated forests (Masters et al. 2018; Sierra et al. 2023). The leaves with iridoplasts have a deep blue color under low light conditions (Jacobs et al. 2016; Castillo et al. 2021). Iridoplasts are formed in shade-adapted plants, absorb light more efficiently than chloroplasts, with a strong blue peak in reflectance at 435–500 nm (Jacobs et al. 2016), and are larger in the presence of stronger blue iridescence (Pao et al. 2018). Preliminary studies suggested that the iridoplast color was a way to attract pollinators or to deter predators (Kirchhoff 2014). However, more recent studies have shown that their main function is to selectively enhance light absorption in low-light environments (Castillo et al. 2021, and other references therein).

Lamelloplasts is another name of iridoplasts. The name is due to the fact that they are modified chloroplasts with regularly spaced concentric lamellar thylakoids (LTs in Figure 1(M)), as in the epidermal cells of shade-dwelling leaves of some species of *Begonia* L. (Pao et al. 2018). The lamellar structure reflects adaptation to low-light conditions, as it enables more efficient light capture and, consequently, a higher photosynthetic rate. In fact, ultrastructural studies have shown that iridescence is affected by the spacing between thylakoid lamellae (Jacobs et al. 2016).

Bisonoplasts are named the iridoplasts present in *Selaginella erythropus* (Mart.) Spring. They show two distinct regions of thylakoid membranes, the lower one with a standard arrangement of grana, and the upper one (facing the adaxial surface of the leaf) with highly ordered thylakoid lamellae (Masters et al. 2018; Sierra et al. 2023).

Kleptoplasty is the capacity of a heterotrophic organism to digest the algal cellular components except the chloroplasts, which are maintained intact and often photosynthetically active (Pierce and Curtis 2012). This action is considered as an endosymbiosis event (McGrath 2020).

Kleptoplasts is the name of the captive chloroplasts.

Some sacoglossan sea slugs can keep chloroplasts alive and photosynthetically active for several weeks or months. This is the reason why they are often referred to as "crawling leaves" and "solar-powered sea slugs" (Cruz and Cartaxana 2022). Kleptoplasty occurs independently in distant protist lineages, including dinoflagellates, ciliates, and foraminifera. Within these protist lineages, the sources of the acquired algal chloroplasts exhibit a diverse origin (Cruz and Cartaxana 2022). In the host organism containing kleptoplasts, reactive oxygen species (ROS) related to the photosynthetic activity are formed and alter the plastid functionality, but also cause damage to the rest of the host organism (Dorrell and Howe 2012). Thus, chloroplast acquisition is a risk for the host, and the actual benefits of possessing kleptoplasts are arguable (Cruz and Cartaxana 2022).

Nitroplasts are named the nitrogen-fixing endosymbiont cyanobacteria, which seem to have acquired organellar characteristics in a marine microalga. Their discovery is very recent (Coale et al. 2024). The strong integration of the endosymbiont in the architecture and functions of the host eukaryotic cell is similar to the plastid model (Coale et al. 2024). This strongly supports that the endosymbiont has been evolved to an organelle (Coale et al. 2024; Massana 2024).

Even if the discovery is limited to microalgae, it is certainly important because it supports the endosymbiotic origin of plastids and adds them new functions.

Altogether plastid classification shows the strong plastidial heterogeneity, putting in evidence aspects of endosymbiont origin, as in the cases of kleptoplasts and nitroplasts, but also of the multiple functionality which leads to intermediate features, as in the case of etio-chloroplasts and amylochromoplasts.

## Plastid interconversion

All plastid types are propagated by the division of pre-existing organelles though a binary fission mechanism using both components inherited from the prokaryotic endosymbiont and factors of eukaryotic origin. The structural dynamism of plastids is also shown by their ability to produce vesicle budding protrusions called stromules (Jarvis and López-Juez 2013, 2014). For example, vesicle budding from the plastid occurs during chromoplast biogenesis in ripening tomato fruits, in endosperm amyloplasts (Forth and Pyke 2006; Pyke 2013), and in tannosomes (Figure 1(K)).

Stromules are tubules with a double-membrane and are stroma-filled (Gray et al. 2011; Pyke 2013). More and longer stromules are present in non-green plastids than in chloroplasts. Stromule frequency is also influenced by developmental and biotic/abiotic stresses, with their abundance increasing also in response to diurnal cycles and hormones, e.g. strigolactones (Hanson and Hines 2018). Stromules are dynamic structures that can rapidly extend, branch or even detach. Stromules have been suggested to facilitate interplastid communication and nuclear/organellar communication (Erickson et al. 2017). They also aid in transport processes because increase the plastid surface area and are involved in autophagy (Ishida et al. 2008; Hickey et al. 2023), as described in a following paragraph.

Plastid phosphatidylglycerol is the major phospholipid of the plastid envelope and of thylakoid membranes. Plastid membrane lipids are galactolipids synthesized by both the prokaryotic and eukaryotic pathways. In the chloroplast, it has been demonstrated that the prokaryotic pathway assembles the FAs synthesized in the plastid; the eukaryotic pathway assembles the plastid-exported FAs into lipids within the

endoplasmic reticulum (ER), and then they are trafficked back to the plastid, where they are converted to monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG), and sulfoquinovosyldiacylglycerol (Chen et al. 2023, and references therein).

Because plastids differ from each other in structure, biochemical activity and functions, their variety implies differences in the expression of both plastid and nuclear genes, as well as a great coordination between plastid and nuclear proteins. Examples of the coordination between plastid transcription machinery and nuclear genome expression are shown for the chloroplast in the following paragraph. A part the peculiar differences, the characteristics of the plastid DNA and a few structural features and functions (such as the biosynthesis of FAs) are shared among all the different plastid types (Sabater 2018). For example, chloroplasts have a small circular genome that varies in size among species, ranging from 107 kb (*Cathaya argyrophylla* Chun & Kuang) to 218 kb (*Pelargonium* × *hortorum* L.H.Bailey), and typically contains 100–250 genes. This genome can be present in multiple copies and in angiosperms is maternally inherited (Daniell et al. 2016). The plastid mRNA distribution is stable for different plastid types, enabling the rapid translation from one to another plastid type (Legen and Schmitz-Linneweber 2017). However, the proteome is different in the different plastid types (Balmer et al. 2006; Siddique et al. 2006; Barsan et al. 2010). For example, a comparative proteomics study in potato revealed that 85 proteins were common in chloroplasts and amyloplasts, including 24 starch metabolism-related proteins, while 1,749 proteins were unique to the chloroplast proteome and 119 proteins were exclusive of the amyloplast proteome (Liu et al. 2022).

Detailed information about proteome peculiarities is available for the chloroplast, but much less for the other plastid types, as summarized in the following paragraphs. However it should be specified that the conversion from one type of plastid to another needs an organellar proteome reorganization with a turnover of plastid proteins, but also a differentially regulated import of nuclear-encoded proteins (Bauer et al. 2000; Soll and Schleiff 2004; Jarvis and López-Juez 2013; 2014; Izumi and Nakamura 2018).

Figure 3 is a schematic representation summarizing the main transition events from one type of plastid to another. The dynamics that characterize the transition are described in the following paragraphs.

## Coordination between plastid transcription machinery and nuclear genome expression: the case of chloroplast biogenesis

Nowadays, in land plants, the organization and expression of the plastid genome remains similar to that of bacteria. For instance, this resemblance is evident in the composition of the translation machinery and the operon-like structure of plastid gene clusters (Zoschke and Bock 2018). As regards chloroplast, this type of plastid possesses different RNA polymerases and a posttranscriptional RNA processing by splicing, editing, end processing, and intercistronic processing that clearly differentiate its gene expression from that of bacteria. These processes were likely established during host-endosymbiont coevolution and are almost all carried out by nuclear encoded protein factors. Moreover, differently from bacteria, the posttranscriptional and translational events are key points in the control of chloroplast gene expression (Zoschke and Bock 2018). At present, numerous plastid genomes have been sequenced, giving information on their organization and evolution in land plants. More than 7700 chloroplast genome sequences are uploaded in the NCBI GenBank Organelle Genome Resources (http://www.ncbi.nlm.nih.gov/genome/organelle/) (Li et al. 2022). Despite variations in plastome size among species, certain genes are consistently retained across most plastomes. This conservation makes them valuable as plastid DNA markers for establishing the phylogeny of numerous plant groups, for delineating species boundaries, and for studying inter-population variation, as established by Li et al. (2022).

In all plastid types of angiosperms several genes are transcribed by at least the plastid-encoded RNA polymerase (PEP), and the nuclear-encoded RNA polymerase (NEP), even if many genes have promoters for both these RNA polymerases. Plastid-encoded RNA polymerase exhibits a bacteria-like core enzyme whose subunits are encoded by plastid genes, whereas the nuclear NEP is a monomeric bacteriophage-type RNA polymerase. Both PEP and NEP are active at all plastidial developmental stages, and their transcriptional activity requires coordination within the plastid and the nucleus, and changes in response to endogenous and exogenous factors, with different degrees of activity according to the developmental stage and physiological condition (Tadini et al. 2020). Moreover, in the case of chloroplast, here described because its plastid genes are highly expressed whereas those of nongreen plastids are drastically downregulated (Li et al. 2022), the plastid biogenesis and functionality also require coordination of the transcription of thousands of nuclear genes with the expression of the relatively few plastid genes through an information flow from developing plastids to the nucleus *via* the retrograde pathway (Tadini et al. 2020). The plastid encoded Genomes Uncoupled 1 protein (GUN1) has been proposed as central node in this signaling. It has features in common with NEP (Tadini et al. 2020).

As described in the following paragraph, when seed germination takes place in darkness, etioplast formation occurs. Etioplasts exhibit a soluble inactive form of the PEP holoenzyme (PEP-B). Upon illumination, the PEP complex interacts with several nuclear PEP-Associated Proteins (PAPs) and becomes part of the membrane-bound plastid Transcription Active Chromosome (pTAC) complex. This complex, named PEP-A, leads to the transcription of the nuclear *Photosynthesis-Associated Plastid-Encoded Genes (PhAPGs)* causing chloroplast formation and activity (Tadini et al. 2020). In the genome of *Arabidopsis thaliana* (L.) Heynh. there are three nuclear genes, called *RPOT*, coding for phage-like RNA polymerases, with two of them targeted to chloroplasts, i.e. *RPOT3*/RpoTp and *RPOT2*/RpoTmp (Tadini et al. 2020). The transcription of these genes is under NEP control, and the knockout of *RPOT2* or *RPOT3* delays chloroplast biogenesis (Tadini et al. 2020).

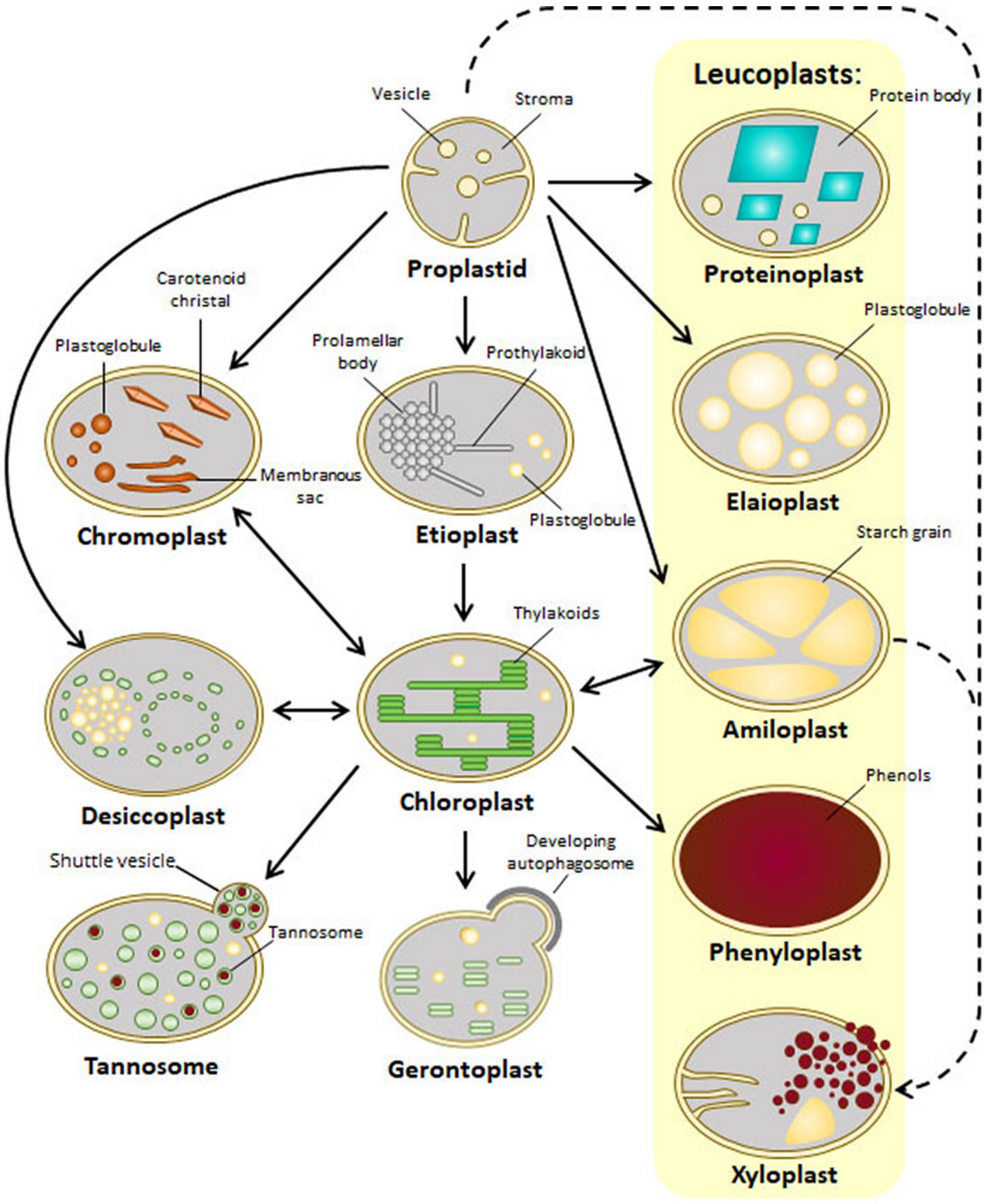


**Figure 3.** Diagram showing the main pathways of plastidial interconversion in angiosperms. Single-headed arrows represent irreversible plastidial transitions (e.g. from proplastid to mature plastid) while double-headed arrows indicate reversible conversions (e.g. from chloroplast to chromoplast and vice versa). The solid lines represent platid transitions that have already been proven while the dotted lines indicate hypothetical transitions (adapted from Pinard and Mizrachi 2018).

In summary, several plastid genomes have been sequenced, with sequencing giving information on plastid organization and evolution. In land plants, chloroplast transcriptome is affected by different RNA polymerases and posttranscriptional RNA processing events. The plastid-encoded PEP and the nuclear-encoded NEP, both plastid RNA polymerases, transcribe numerous genes, contributing to the complexity of plastid transcription. The plastid encoded GUN1 protein seems to be a central node in the coordination of the information flow between the young plastid and the nucleus through the retrograde pathway (see Introduction).

## Proteomic insights into plastid behavior

Today's chloroplast proteome comprises several thousand proteins, predominantly encoded by the nucleus and imported posttranslationally into the organelle (Zoschke and Bock 2018). Meanwhile, approximately 90 proteins are encoded within the plastid itself (Mohanta et al. 2022).

AT_CHLORO (www.grenoble.prabi.fr/at_chloro) is an important database dedicated to the chloroplast proteome of *Arabidopsis thaliana* (L.) Heynh. It contains information for the proteins of the envelope, stroma, and thylakoids (Bruley et al. 2012). More recently, the chloroplast proteome of just under three thousand species, including algae, protists and land plants, has been analysed, and a virtual 2D map constructed (Mohanta et al. 2022). The map shows that the molecular mass of the chloroplast proteome ranges from 0.448 to 616.334 kDa, and the isoelectric point (pI) from 2.854 to 12.954, with both molecular weight and pI showing a bimodal distribution. The basic pI proteins are predominant, and leucine is the most abundant amino acid and cysteine the least abundant amino acid in the chloroplast proteome, even if the highest and lowest amino acid abundance partially depends on the taxonomic rank. By principal component analysis (PCA) of the low-molecular-mass proteins it has been shown that monocots, magnoliids, gymnosperms, and bryophytes share similar low-molecular-mass chloroplast proteins, while the low-molecular-mass proteins of eudicots, Nymphaeales, pteridophytes, and algae cluster separately (Mohanta et al. 2022). Nonetheless, the chloroplast proteome includes small peptides (Mohanta et al. 2022) and exhibits a higher proportion of basic pI proteins (about 56%) compared to those encoded by the nucleus. Given the alkaline pH environment of the chloroplast stroma, it has been proposed that this higher proportion of basic pI proteins aids in maintaining homeostasis (Mohanta et al. 2022).

To thrive on land, plants required elaborate signaling pathways to react to diverse environmental conditions and to control developmental programs. Thus, the conquest of land by plants required the subfunctionalization into specialized heterotrophic plastid types, e.g. the chromoplasts, exhibiting large disparities in metabolic functions, and a targeted use of amyloplasts, to accumulate reserves in non-photosynthetic organs and to respond to the force of gravity. However, even if with a long history, the characterization of the various metabolic properties of these and the other types of non green plastids is still far from being accomplished (Kuntz et al. 2024). In fact, the study of their proteomes is limited, being known only for *Triticum aestivum* L. amyloplasts, *Oryza sativa* L. etioplasts, *Fortunella margarita* (Lour.) Swingle elaioplasts and *Nicotiana tabacum* L. proplastids (Li et al. 2022). Of course, the proteome of a specific plastid type reflects its prevalent functioning. As detailed in the following paragraphs, for example, chromoplasts are enriched in carotenoid synthesis and storage proteins, elaioplasts are very active in terpene synthesis (Zhu et al. 2018), amyloplasts in carbohydrate metabolism, lipid and amino acid biosynthesis proteins (Balmer et al. 2006; Dupont 2008). About the similarities, it is possible to say that all non-green plastids show an enrichment of carbohydrate metabolism enzymes, abundant heat shock proteins and redox enzymes (Christian et al. 2023). However, even if recently updated (Christian et al. 2023), a comprehensive overview of the proteome of each plastid type and of the proteomic similarities among different plastids is still far to be completed, and differences between published data enhance confusion.

In summary, the chloroplast proteome has been extensively studied. The majority of its proteins are encoded by the nucleus and are posttranslationally imported into the organelle. Basic proteins are prevalent, with leucine being the most abundant amino acid and cysteine the least abundant, although their abundance varies depending on the taxonomic rank.

By contrast, the study of the proteomes of the heterotrophic plastids is still limited, and a comprehensive overview of the proteome of each of these plastid types and of their proteomic similarities is still lacking. As also proposed by other authors (Christian et al. 2023), this investigation is critically needed to gain a holistic view of plastid proteomics.

## Proplastids and chloro-etioplasts/etioplasts conversion into chloroplasts

Chloroplast development usually proceeds from proplastids (Liang et al. 2018). Nevertheless, pathways for conversion, whether direct or indirect, related to etioplasts or to stages of etio-chloroplasts, have also been documented (Solymosi and Schoefs 2010).

In the absence of light, the development of the proplastid into a chloroplast does not start and the proplastid is converted into an etioplast (Solymosi and Schoefs 2008). In etioplasts, the PLB is joined continuously with flattened porous tubular PTs (Figure 1(G)) (Gunning 2001). The etioplast contains low amounts of a chlorophyll precursor, named protochlorophyllide (Pchlide), and carotenoids (Schoefs and Franck 2003; Masuda and Takamiya 2004; Masuda 2008). In comparison with the chlorophyll content of light-grown plants, the Pchlide content is two–three orders of magnitude smaller. However, proteomic analyses on isolated PLBs (Blomqvist et al. 2008) have shown the presence in the PLB-membranes of several proteins involved in photosynthesis. This supports the notion that they are precursors of the chloroplast thylakoids and that during the greening process they will be used for photosynthetic membrane formation (Solymosi and Schoefs 2010).

Both proplastid-to-chloroplast and etioplast-to-chloroplast transitions occur naturally during plant development, however they have different dynamics and follow different schemes of structural transformations.

Membrane development from the simple tubulo-vesicular PTs of the proplastids to the membrane system of the chloroplast is longer compared to what happens in the etioplast-to-chloroplast transition due to the limited lipid and protein presence in proplastids, which, instead, are abundant in the PLB of the etioplast (Gunning 2001; Kleffmann et al. 2007; Blomqvist et al. 2008). Moreover, as shown by Liang et al. (Liang et al. 2018) in greening Arabidopsis cotyledons, the tubulovesicular PTs must be transformed into sheet-like

thylakoids connected locally with the inner envelope membrane for the complete chloroplast biogenic process to occur. The flattening membranes must develop a narrow lumen and may be accompanied by polysome binding.

Upon illumination during plant greening or de-etiolation, the etioplast-to-chloroplast transition occurs and involves the transformation of the PLB into grana-stroma thylakoid arrangement (Mostowska 1986; Von Wettstein et al. 1995). Transformation of the paracrystalline structure of the PLB into an irregular one runs in parallel to the phototransformation of Pchlide to chlorophyllide (Chlide) (Selstam et al. 2002). The PLB transformation into lamellar thylakoids via vesicle dispersion has been well described in isolated wheat PLBs (Kowalewska et al. 2016). Changes in the activity of Phytoene Synthase (PSY), the enzyme catalysing the first step of carotenoid biosynthesis, alter carotenoid composition and plastid differentiation, demonstrating the importance of carotenoids in the etioplast/chloroplast transition. In accordance, in *Arabidopsis thaliana* (L.) Heynh. *there are mutants in which cis*-carotene accumulation is enhanced and this triggers a *cis*-carotene-derived apocarotenoid signal that blocks the PLB formation in the etioplasts and causes development of pseudochloroplasts (Hou et al. 2024).

Moreover, during the light period of light/dark cycles cells with intense exogenous secretory functions, e.g. biosynthesis of terpenes, may contain plastids with PLB-like structures (Turner et al. 2000; Stpiczynska et al. 2005; Tollsten and Bergström 2008). In some cases, PLBs appear during the dark period of the light/dark cycles but are absent under continuous light, as observed in the glandular hairs of *Perilla ocymoides* L. (Kashina and Danilova 1993). In addition, at early stages of seedling development or under white or monochromatic light of low intensity, dispersed internal plastid membranes of the PLB retain the potential to recrystallize into a PLB lattice (Schoefs and Franck 2008; Rudowska et al. 2012). However, the recrystallization process depends on the plant species (Kowalewska and Mostowska 2016). Furthermore, the PLBs that are formed during long periods of etiolation show a slower tubular-lamellar transition or disintegration when exposed to illumination as compared to those formed during short dark periods.

In the first leaves of epigeal germinating runner bean, after the first hour of illumination, the PLB structure becomes irregular, with membranes at its margin giving rise to flat stromal slats. All membranes directly transform from one arrangement into another, i.e. tubular structures directly into porous flat slats (Kowalewska et al. 2016). During the subsequent hours of illumination PLB degradation continues with the porous PT membranes becoming arranged parallel to each other and to the long chloroplast axis (i.e. like in pregranal plastids). After 8 h of illumination, the first stacked non-porous membranes in continuity with PTs are detected giving rise to grana formation (Kowalewska et al. 2016). Even if initially expanded in the lateral rather than vertical direction, during further growth, grana increase in height and become more regularly arranged and more stacked reaching the repeat distance values characteristic for grana in fully developed plants (Kowalewska et al. 2016).

Collectively, irrespective of the preliminary form of the internal plastid membrane system (i.e. tubulovesicular PTs in proplastids or PLB in etioplasts) as well as of the dynamics of chloroplast biogenesis, in both cases of transition the light-induced transformation of the membrane arrangement leads to the formation of the thylakoid network built by helical grana connected via stroma thylakoids arranged parallel to each other (Kowalewska et al. 2016; Liang et al. 2018).

Plastoglobules are thylakoid-associated lipid droplets, consisting of a membrane lipid monolayer surrounding a core of neutral lipids. They actively participate in thylakoid function from biogenesis to senescence, acting in metabolite synthesis, repair and disposal under changing environmental conditions and developmental stages. Plastoglobules are also involved in the conversion from one plastid type to another (Rottet et al. 2015). The PLB of the etioplast shows numerous PGs interdispersed with the tubular structures (Lichtenthaler 1968). Following light exposure, the de-etiolated tissues show a decrease in the number of PGs and a concomitant increase in thylakoid membranes derived from the PLB (Lichtenthaler and Peveling 1966; Nacir and Bréhélin 2013).

Plastoglobules, being a lipid reservoir, assist in the rapid formation of thylakoid membranes in greening tissues by releasing structural thylakoid lipids (MGDG) and their precursors [triacylglycerol (TAG), and diacylglycerol]. They also contain tocopherol and other prenylquinones, therefore they are also involved in protecting the nascent membranes of the chloroplast by supplying lipid antioxidants (Piller et al. 2014).

In the chloroplast, PGs are mainly located at the curved regions of the thylakoid membranes (Austin et al. 2006) and become larger and more abundant in the mature organelle in comparison with the nascent one (Lichtenthaler 1968). The membrane lipid surface, continuous with the thylakoid outer leaflet, is studded with proteins (Kessler et al. 1999). Many of the PGs are implicated in lipid synthesis and metabolism (Vidi et al. 2006; Ytterberg et al. 2006; Grennan 2008; Lundquist et al. 2012; Piller et al. 2012). Because of their close connection with thylakoids, PGs are considered as an integral structural element of grana (Kowalewska et al. 2019), but also exhibit a role in lipid remodeling during the conversion from one plastid type to another. Plastoglobules are also thought to allocate stored electron carriers to the membranes, contributing to the electron carrier synthesis and metabolism (Venkatasalam et al. 2022).

Summarizing, light is the crucial factor that influences proplastid and etioplast conversion into a chloroplast. Under high light intensity, proplastids differentiate directly into chloroplasts. When light intensity is low or absent, proplastids differentiate into either etio-chloroplasts or etioplasts, developing PLBs in both cases. This occurs because the formation of chlorophyll-proteins complexes, and related functioning, is inhibited by the strong reduction/absence of light, but not lipid biosynthesis, which thus allows PLB formation (Solymosi and Schoefs 2010). However, both etio-chloroplasts and etioplasts are converted into chloroplasts, when light conditions become favorable, and with an important role played by the dismantling of PLBs.

Moreover, the low light/no light-induced conversion of the chloroplast into the etio-chloroplast and then the etioplast,

again involves PLB formation, as consequence of a continuously active lipid biosynthesis in contrast with a progressively reduced photosynthesis. In accordance, under light/dark cycles the young chloroplasts form PLBs during the dark period of each cycle, which dismantle under the light period, and this, lasts up to their maturation.

## Origin and dynamics of chromoplasts

### *Chromoplast to chloroplast interconversion*

Even if important crops such as *Hordeum vulgare* L., *Zea mays* L., *Solanum tuberosum* L., and *Manihot esculenta* Crantz synthesize and store carotenoids in the amyloplasts of the edible organs (Li and Yuan 2013), chromoplasts are the most important carotenoid-starving organelles. In addition, the chromoplast has been suggested to be the most recently evolved plastid type (Kuntz and Rolland 2012).

The control of chromoplast biogenesis is a key factor for the regulation of the content of carotenoids in plants, facilitating their extensive biosynthesis and substantial storage capacity (Lu and Li 2008; Cazzonelli and Pogson 2010; Ruiz-Sola and Rodríguez-Concepción 2012). Carotenoid accumulation is determined by the rate of biosynthesis and degradation, as well as by the capacity of a stable accumulation of the synthesized compounds. Chromoplast biogenesis is linked with membrane proliferation and re-modelling of the internal membrane system to develop carotenoid-lipoprotein sequestration substructures as well as PGs (Egea et al. 2010). Chromoplast substructure formation and acquisition of new biosynthetic capacity are allowed by the plastid envelope membrane budding or fusion (Camara et al. 1995). Membranes are either newly synthesized from vesicles derived from the inner plastid membranes during chromoplast biogenesis (Simkin et al. 2007) or derive by the partial disassembly of the membranes of the organelle from which the chromoplast is derived. Membranes are also able to proliferate during chromoplast differentiation, as in *Narcissus pseudonarcissus* L. flowers (Kleinig and Liedvogel 1980).

Chromoplasts derive from either proplastids or pre-existing leucoplasts but mainly from chloroplasts (Figures 2(J) and 3). This conversion occurs because in the chloroplasts, carotenoids constitute photosynthetic complexes in thylakoid membranes (Cazzonelli and Pogson 2010; Ruiz-Sola and Rodriguez-Concepcion 2012), and their composition and abundance are related to the optimal function of photosynthesis, with lutein, β-carotene, violaxanthin, and neoxanthin as dominant carotenoids (DellaPenna and Pogson 2006). The prevalent development from chloroplasts occurs because carotenoids are not synthesized in the proplastids (Howitt and Pogson 2006), the etioplasts have low biosynthetic catalytic activity and storage capacity of carotenoids (Toledo-Ortiz et al. 2010), and amyloplasts lack carotenoid sequestering structures (Lopez et al. 2008), and consequently, crops such as *Triticum aestivum* L., *Hordeum vulgare* L., *Zea mays* L. and *Solanum tuberosum* L. have generally low contents of carotenoids in the amyloplasts of seeds or roots (Howitt and Pogson 2006).

Thus, depending on their origin, in the chromoplasts, carotenoid content and identity vary largely from negligible in white organs to very high quantity in colored organs, which accumulate carotenoids such as lycopene in *Citrullus lanatus* (Thunb.) Matsum. & Nakai and *Solanum lycopersicum* L. fruits, α-/β-carotene in *Daucus carota* L. and *Ipomoea batatas* (L.) Lam., and lutein in Calendula officinalis L. flowers (Li and Yuan 2013, and other references therein).

Chromoplasts are classified into globular, crystalline, membranous, fibrillar, and reticulo-tubular types based on the variation of their substructures (Camara et al. 1995; Egea et al. 2010). However, more than one type of carotenoid sequestering substructures is often found within a chromoplast.

Globular chromoplasts are the simplest and most frequent type (Figure 2(D)). They are characterized by an accumulation of PGs, and are present in numerous fruits and vegetables, such as *Citrus paradisi* Macf., *Cucurbita moschata* Poir, *Mangifera indica* L., and *Carica papaya* L. (Vasquez-Caicedo et al. 2006; Schweiggert et al. 2011; Jeffery et al. 2012; Li and Yuan 2013). In *Viola tricolor* L. PGs consist of a central anisotropic core of xanthophylls esterified with FAs and arranged in a chaotic manner surrounded by a monolayer of polar lipids and structural proteins (Hansmann and Sitte 1982).

Crystalline chromoplasts are normally associated with hyperaccumulation of β-carotene and lycopene as crystal structures (Figure 2(B)) and are typically found in *Daucus carota* L. root and *Carica papaya* L. (Kim et al. 2010; Schweiggert et al. 2011; Jeffery et al. 2012). They contain large carotenoid crystals inserted in the lumen of overlapping membrane sacculi formed mainly by introflections of the inner envelope membrane.

Membranous chromoplasts (Figure 2(C)) contain low amounts of PGs and are characterized by concentric membranes proliferating from the plastid inner envelope membrane, such as in *Capsicum annuum* L. fruits. In the latter, during the transition to fully mature chromoplasts, it has been noted that important components of the chloroplast, i.e. the cytochrome b6f complex, the ATPase complex, and the enzymes involved in the Calvin Benson cycle are consistently preserved at elevated levels, while the two photosystems disassemble and their components degrade (Rödiger et al. 2021). The membrane lamellae have a high lipid/protein ratio and contain about 3% carotenoids. In *Narcissus pseudonarcissus* L. the carotenoids consist essentially of xanthophylls, such as lutein, violaxanthin and neoxanthin, already present in the chloroplast (Alpi et al. 1995). In the flowers of this species chromoplasts display respiratory activity by converting oxygen into water and producing ATP (Grabsztunowicz et al. 2019).

*Fibrillar chromoplasts* show the presence of lipoprotein fibrils with extensive bundled microfibrillar structures, as in *Capsicum annuum* L. (Deruère et al. 1994). In this plant, a model for fibril architecture has been proposed. According to the model, carotenoids accumulate in the center of the fibrils in parallel rows and are surrounded by a layer of polar lipids. This layer is in turn surrounded by an outer layer of fibrillin. Moreover, the carotenoid containing fibrils and internal membranes arise in the presence of chlorophyll-containing

thylakoids supporting that thylakoids remain preserved despite carotenoid accumulation and fibril formation. This implies that fibril formation occurs *de novo* and does not depend on molecules released from deteriorating thylakoid membranes (Deruère et al. 1994).

*Reticulo-tubular* chromoplasts contain stroma filled by a twisted fibril network together with few PGs, e.g. in *Tulipa gesneriana* L. (Camara et al. 1995) and *Mangifera indica* L. (Vasquez-Caicedo et al. 2006). In the latter plant, a transmission electron microscopy study showed that the mesocarp cells of the fruit exhibited chromoplasts with PGs together with tubular membranes with and without electron dense contents. These tubular membranes were present as both single tubules and characteristic networks (Vasquez-Caicedo et al. 2006).

Chromoplasts with more than one specific characteristic have also been described. For example, *Capsicum annuum* L. and *Solanum lycopersicum* L. fruits exhibit chromoplasts with both globular and membranous features (Summer and Cline 1999; Angaman et al. 2012). The most conspicuous processes that occur early during the chloroplast-to-chromoplast transition are an increase in carotenoid and quinone contents and a fibril assembly and degradation of thylakoids (Ljubesić et al. 1991). In addition, as in *Solanum lycopersicum* L., the inner envelope membrane and thylakoid membranes vanish during the transition of chloroplasts into chromoplasts, and PGs and crystals are formed through membrane fusion and vesicle budding (Brehelin et al. 2007; Zita et al. 2022).

Thus, chromoplasts are characterized by the disassembly of chloroplast thylakoids and an abundance of carotenoids stored and produced in PGs or carotenoid fibrils with the help of ζ-carotene desaturase, lycopene β-cyclase and two β-carotene β-hydroxylases. The latter ones catalyze the conversion of β-carotene into xanthophylls (Li and Yuan 2013). Carotenoid cleavagedioxygenase4 cleaves carotenoids to release apocarotenoids that contribute to scent and flavor (Rottet et al. 2015).

The first step of the carotenoid pathway is the conversion of geranylgeranyl di-phosphate to phytoene, catalyzed by phytoene synthase (referred to crtB in bacteria) (Llorente et al. 2020). It has been demonstrated that the bacterial crtB enzyme induces the transformation of chloroplasts into chromoplasts in the leaves of numerous plants (*Nicotiana tabacum* L., *Nicotiana benthamiana* Domin, *Arabidopsis thaliana* (L.) Heynh.). This "synthetic" conversion clearly demonstrates that the buildup of carotenoids and the structural changes associated with the chloroplast-to-chromoplast transformation involve a reorganization of the plastid protein content, and a global reprogramming of nuclear gene expression and primary metabolism (Llorente et al. 2020).

The PGs of chromoplasts are larger than those of chloroplasts and contain less xanthophyll esters than those of gerontoplasts (Mulisch and Krupinska 2013).

Summarizing, chromoplast differentiation from chloroplasts involves the degradation of chlorophyll and disappearance of thylakoid structures, and is accompanied by the remodeling of internal membrane systems and accumulation of carotenoids in the newly formed carotenoid sequestering substructures (Egea et al. 2010; Bian et al. 2011). The process of transition from chloroplasts to chromoplasts in petals shares great similarity with that occurring in the fruits. In the transition from chloroplast to chromoplast during fruit ripening the breakdown of chlorophyll-containing thylakoid membranes and the chromoplast membranes formation are independent processes (Cheung et al. 1993). Moreover, during *Solanum lycopersicum* L. fruit ripening, plastids containing both carotenoids and chlorophylls at the breaker stage have been found (Egea et al. 2011).

The process from chloroplast to chromoplast is irreversible in *Solanum lycopersicum* L. (Egea et al. 2011; Barsan et al. 2012; D'Andrea et al. 2014), *Capsicum annuum* L. (Jeong et al. 2020), *Arum italicum* Mill. (Bonora et al. 2000), and *Lilium longiflorum* Thunb. (Juneau et al. 2002). However, it is not terminal in organs of other plants in which the fully differentiated chromoplasts can re-differentiate into chloroplasts (Li and Yuan 2013). The reversion from chromoplast to chloroplast may be also caused by environmental cues, as exemplified by the leaves of the *Buxus sempervirens* L. These leaves become red in autumn and winter due to the synthesis of red carotenoids as a response to the photo-inhibitory conditions during winter acclimation and turn green in spring on exposure to warmer temperatures (Hormaetxe et al. 2004). This is because the chloroplasts are changed into globular chromoplasts in autumn/winter and are restored as chloroplasts in spring (Koiwa et al. 1986).

Regreening is the reversible change from chromoplast to chloroplast. Examples are given by *Citrus sinensis* L. (Mayfield and Huff 1986), *Cucurbita pepo* L. *var. ovifera* (L.) Alef. (Devidé and Ljubešić 1974), and *Cucumis sativus* L. fruits (Prebeg et al. 2008). During regreening, thylakoids reconstitution starts with the formation of membrane-bound bodies, followed by their expansion and fragmentation up to double-membrane sheets formation. Interestingly, PGs remain visible during the reconstruction. The chromoplast-to-chloroplast transition implies the association of numerous types of membrane structures with the plastid envelope (Prebeg et al. 2008). Light greatly affects regreening and the increase in chlorophyll content (Ma et al. 2021). For example, the conversion from β-carotene-rich chromoplasts to lutein-containing chloroplasts is induced by the exposure to light in *Daucus carota* L. roots (Rodriguez-Concepcion and Stange 2013). However, other factors may be involved in this process, e.g. in *Citrus unshiu* (Mak.) Marc. fruits. They include an excess of nitrogen, treatments with exogenous gibberellin, high temperatures and the spectral composition of the light (blue component) (Sadali et al. 2019; Ma et al. 2021; Keawmanee et al. 2022).

## *Differentiation of chromoplasts from other plastid types*

The *Brassica oleracea* L. var. *botrytis* DC. orange curd mutant is an example of chromoplast differentiation from proplastids. The mutant accumulates high levels of carotenoids in shoot apical meristems. These carotenoids are contained in chromoplasts, which are the only plastid type present in the apex, whereas the wild-type shoot apices contain multiple proplastids, supporting a chromoplast origin from proplastids (Paolillo et al. 2004). In accordance, in *Arabidopsis thaliana* (L.) Heynh. callus, proplastids can be converted into chromoplasts (Choi et al. 2021, and other references therein).

The transition from proplastid to chromoplast may be found also during fruit maturation, e.g. in *Citrullus lanatus* (Thunb.) Matsum. & Nakai (Fang et al. 2020*), Carica papaya* L. (Schweiggert et al. 2011), and in *Daucus carota* L. calli (Oleszkiewicz et al. 2018).

In *Citrullus lanatus* (Thunb.) Matsum. & Nakai, chromoplast differentiation and carotenoid accumulation occur during the maturation of the fruit, and the number of PGs in the chromoplasts affects fruit color at maturity. In fact, the PG number is higher in the red-fleshed ("LSW-177") accession of *Citrullus lanatus* (Thunb.) Matsum. & Nakai than in the yellow and orange ones, "PI 635597" and "PI 192938" accessions respectively, and the latter two show a higher number of PGs than the white-fleshed ("PI 186490") accession (Fang et al. 2020). This may occur also in *Daucus carota* L. callus. In fact, in pale-yellow calli the carotenoid content is low and proplastids are present. Conversely, chromoplasts with high carotenoid contents, are largely present in dark orange calli, where proplastid number is highly reduced (Oleszkiewicz et al. 2018).

During fruit and root development, chromoplasts may also derive from leucoplasts present in young, non-photosynthetic tissues. For example, leucoplasts are found to be among the dominant plastids in unripe *Carica papaya* L. fruits, and chromoplasts differentiate directly from these plastids or from proplastids (Schweiggert et al. 2011). Similarly, chromoplasts differentiate from amyloplasts in *Daucus carota* L. roots during the organ development (Ben-Shaul and Klein 1965), with the transition occurring concomitantly with the beginning of carotenoid accumulation (Kim et al. 2010).

Chromoplasts in red stigmas of saffron (*Crocus sativus* L.) evolve from amyloplasts because these are the only plastids present in the colorless basal part of the saffron style, and amylo-chromoplasts, as transition forms of plastids, may be also present (Grilli Caiola and Canini 2004). When *Nicotiana tabacum* L. floral nectaries change to orange color, chromoplasts directly differentiate from amyloplasts, with the conversion process accompanied by the breakdown of starch and the production of nectar sugars (Horner et al. 2007).

The endosperm of *Oryza sativa* L. caryopses is formed by amyloplasts and does not produce significant amounts of carotenoids. However, the overexpression of carotenogenic genes such as *ORANGE* (*OR*), *deoxy-D-xylulose 5-phosphate synthase* (*DXS*), *PSY*, and *bacterial phytoene desaturase* (*CRTI*) results in chromoplast development even in caryopses (Ye et al. 2000; Wurtzel et al. 2012; Bai et al. 2016; You et al. 2020).

Summarizing, chromoplasts derive from proplastids during fruit maturation and in calli produced through culture *in vitro*. Chromoplasts may also derive from leucoplasts during fruit and root development, and from amyloplasts, e.g. in stigmas and floral nectaries.

## Genetic, metabolic and ROS control of chromoplast differentiation

Regardless of its origin, the differentiation of chromoplast structures requires a change in the developmental program of the organelle determined by both endogenous and environmental information.

In addition to the genes involved in the breakdown of the photosynthesis machinery, several other factors control chromoplast differentiation. For example, in *Capsicum annuum* L., during the chloroplast-to-chromoplast transition plastid fusions and/or translocation factors (PFTFs) has been found to be involved in vesicle fusion and internal plastid remodeling (Hugueney et al. 1995). Moreover, while plastome gene expression is suppressed in mature chromoplasts, it continues to be active during their differentiation. The expression of photosynthesis-related proteins is down-regulated at the translational level (Kahlau and Bock 2008), but the gene expression for FA biosynthesis is maintained (Kahlau and Bock 2008; Egea et al. 2010), because it is indispensable for the reorganization of the internal membranes of the chromoplast in advance of carotenoid synthesis (Barsan et al. 2012).

Chromoplasts contain an endogenous functional ATP synthesis system. In accordance, elevated ATP production is found to be associated with chromoplast differentiation during the chloroplast to chromoplast transition and ATP synthase and adenine nucleotide translocator are among the most abundant proteins in the chromoplast proteome in various crops (Wang, Yang, et al. 2013).

Temperature is among the environmental parameters affecting chromoplast formation, with optimal temperature conditions important for optimal organelle differentiation. This is true particularly in temperature-sensitive fruits such as *Solanum lycopersicum* L. and *Carica papaya* L., to ensure constancy in color (Sadali et al. 2019, and references therein).

The role of ethylene induced *Apetala2a* (*AP2a*) gene in the onset of chromoplast differentiation has been suggested, because the disrupting of its expression perturbs carotenoid biosynthesis causing yellow rather than red fruits, e.g. in *Solanum lycopersicum* L. (Karlova et al. 2011). Interestingly, AP2a has been shown to up-regulate heat-shock protein 70 (Hsp70), which acts in the cytosol as a chaperone for plastid protein import, thus facilitating the import changes necessary to chromoplast transition (Karlova et al. 2011).

The MADS-box transcription factor RIPENING INHIBITOR, together with TOMATO AGAMOUS LIKE1, are positively involved in the regulation of rate-limiting enzymes in carotenoid pathways in *Solanum lycopersicum* L. fruit ripening (Itkin et al. 2009; Martel et al. 2011; Lü et al. 2018). The transcription of *PSY* and of phytoene desaturase (*PDS)*, rate-limiting enzymes in carotenoid biosynthesis, is activated by the light-induced bZIP transcription factor LONG HYPOCOTYL 5 (HY5) (Toledo-Ortiz et al. 2014). Another positive regulator is OR, which is involved in the generation of chromoplasts in the floral organs of *Brassica oleracea* L. var. *botrytis* (Li et al. 2003; Lu et al. 2006) and other species (Kim et al. 2018; Welsch et al. 2019). OR enhances the PSY protein stability and increases its activity (Welsch et al. 2018). Moreover, the exogenous induction of rate-limiting carotenoid biosynthesizing enzymes triggers the plastid conversion to chromoplasts (Ha et al. 2019; Llorente et al. 2020) further confirming the pivotal role of genes of carotenoid biosynthesis in inducing chromoplast development (Bouvier et al. 1998; Sadali et al. 2019; Choi et al. 2021, and other references therein).

It is widely known that FA biosynthesis and lipid metabolism are critical for membrane proliferation, and that lipids

are essential for the carotenoid-lipoprotein sequestration substructures and for PGs in chromoplasts. In accordance, a large number of proteins involved in lipid metabolism, including key enzymes for the synthesis of FAs, sulfolipids, and glycolipids and for lipid catabolism and homeostasis have been identified in the chromoplast proteome in various crop species (Wang et al. 2013b).

The accumulation of sugars is concomitant with carotenoid accumulation and chromoplast differentiation in maturing fruits and in roots. Several studies provide evidence that sugars play important roles in stimulating chromoplast biogenesis and carotenoid accumulation (Huff 1983; Iglesias et al. 2001; Horner et al. 2007). For example, chromoplast differentiation in citrus fruit epicarp is stimulated by sucrose, with high sucrose supplementation promoting the conversion of chloroplasts into chromoplasts, and sucrose depletion reversing the process (Iglesias et al. 2001).

A positive correlation between increased levels of sucrose and reducing sugars with carotenoid accumulation and chromoplast formation has been observed also during tobacco nectary development, where chromoplast differentiation from amyloplasts is associated with starch degradation and production of nectar sugars (Horner et al. 2007). Similarly, during *Solanum lycopersicum* L. fruit ripening and in *OR* transgenic potato tubers, chromoplast differentiation and carotenoid accumulation are correlated with the declining of plastid starch content and progressive conversion into reducing sugars (Thom et al. 1998; Luengwilai and Beckles 2009a, 2009b; Li et al. 2012).

It is well known that ROS are central players in the complex signaling network of cells for example in inducing chromoplast-specific carotenoid gene expression during chromoplast differentiation. In fact, ROS play a vital role in coordinately activating numerous morphological and biochemical changes, leading to the transition into chromoplasts (Bouvier et al. 1998).

ROS homeostasis is maintained by redox system enzymes, many of which, such as ascorbate peroxidase, glutathione reductase, glutathione peroxidase, and superoxide dismutase, identified in the chromoplast proteome, are abundant in these plastids (Barsan et al. 2010, Zeng et al. 2011; Wang et al. 2013b) and their increase is involved in chloroplast- to-chromoplast transition, e.g. in *Solanum lycopersicum* L. and *Capsicum annuum* L. fruits (Martí et al. 2009; Barsan et al. 2012).

Summarizing, regardless of its origin, chromoplast differentiation requires strong changes in the developmental program. The plastome gene expression is suppressed only in the mature chromoplast. Chromoplast differentiation is modulated by temperature. The genes of the carotenoid biosynthesis exhibit a pivotal role in inducing chromoplast development. The accumulation of sugars is concomitant with carotenoid accumulation during chromoplast differentiation in maturing fruits and in roots. Numerous proteins involved in lipid metabolism have been identified in the chromoplast proteome of some species. ROS play a vital role in coordinately activating the morphological and biochemical changes for chromoplast differentiation and maintenance.

## Origin and dynamics of amyloplasts

Amyloplasts are a subtype of leucoplasts (Figure 3). Amyloplasts are common in seeds/caryopses, tubers, and roots for organic carbon storage, but they are also often found in various tissues of leaves and stems for a temporal storage (Jarvis and López-Juez 2013, 2014), and rarely are present in fruits. Amyloplasts are composed of an outer envelope membrane, an inner envelope membrane and an internal stroma containing the starch synthesis machinery (Tetlow and Emes 2017).

Thus, they are characterized by the presence of granules that synthesize and store starch, named storage starch (Esau 1965), at high density and for a long time (Figure 2(E,K)). Starch granules are also found inside the chloroplasts because assimilation starch (Esau 1965) is the direct product of photosynthetic activity. However, the presence of assimilation starch in the chloroplast is transient, in fact it is degraded by hydrolysis to metabolites that can be exported from the chloroplast to the cytosol.

Many starch granules are formed within a single amyloplast, and the amyloplast envelope begins to degrade after the amyloplast becomes full of starch granules (Wei et al. 2008). Moreover, during seed desiccation, e.g. in maize, it has been demonstrated that the lipids associated with the starch granule surface come from the degrading amyloplast bilayer lipid membrane (Tan and Morrison 1979).

Cereal endosperm accumulates high levels of starch in amyloplasts, which are characterized by variable dimensions among species, e.g. *Oryza sativa* L., *Hordeum vulgare* L. and *Zea mays* L. (Matsushima et al. 2010).

The starch grain is called compound grain when the amyloplast contains a single grain that is assembled of several dozen smaller starch granules, with each granule with a diameter of 3–8 µm (Matsushima and Hisano 2019). In a compound grain, starch granules are not fused, thus can be easily separated. By contrast, only one granule is present in simple starch grains. Simple grains are produced in several cereals, such as *Zea mays* L., *Sorghum bicolor* (L.) Moench, *Hordeum vulgare* L., and *Triticum aestivum* L. In the latter two species two discrete size classes are present in the same cells (Matsushima et al. 2014, and references therein). For example, the endosperm of some *Triticum aestivum* L. cultivars contains A-type granules that are lenticular, large in size (>9.9 µm) and are initiated early in the grain filling period, and B-type starch granules that are smaller in size (<9.9 µm) and are initiated during the later stages of grain filling, even if also irregular small C-type starch granules are occasionally present (Peng et al. 1999, Ma et al. 2018).

The number of plastid DNA copies per amyloplast is variable and changes with time. During wheat endosperm development it increases from ~ 10 copies at 9 days after anthesis (DAAs) to ~ 50 copies at 31 DAAs, when the amyloplast becomes mature (Ma et al. 2018 and other references therein). Moreover, the differential expression of nucleic acid-related proteins seems to be related to the different number of plastid DNA copies present in the amyloplast. In fact, it has been suggested that some functions related to starch accumulation in amyloplasts require proteins encoded by the plastid genome (Wang et al. 2016).

In addition, there are functional connections between starch biosynthesis and the structure of internal amyloplast membranes, which are specifically related to the synthesis of galactolipids (Myers et al. 2011). In *Oryza sativa* L. endosperm, various regulatory processes in the amyloplast stroma control ADP-glucose flux into starch (Cakir et al. 2016).

By analogy with chloroplasts and etioplasts, amyloplasts are involved in many metabolic processes in addition to starch production. For example, in the caryopses of *Triticum aestivum* L. it has been shown that amyloplasts play a central role in the endosperm metabolism necessary to transform the imported sucrose, glutamine, and a few other amino acids, into different amino acids, lipids, nucleic acids and carbohydrates needed for starch and protein accumulation and for the interaction with the environment (Dupont 2008). However, many functions are genotype-specific, as in *Triticum aestivum* L. hard and soft cultivars, and others are related to the origin of the amyloplast (Ma et al. 2018, and references therein).

It is interesting that in some cases the amyloplasts are not stable structures, for example in *Arabidopsis thaliana* (L.) Heynh. leaves (Fernandez et al. 2017). In addition, unlike other plastid types, amyloplasts may coexist with other plastid types, such as chloroplasts (Figure 2(K)) or chromoplasts (Figure 2(B,E)), and intermediate forms between chloroplasts and amyloplasts, e.g. in *Marchantia polymorpha* L. (chloro-amyloplasts), or between chromoplasts and amyloplasts (amylo-chromoplasts), e.g. in *Cucurbita maxima* Duchesne and *Bactris gasipaes* Kunth fruits and *Ipomoea batatas* (L.) Lam. tuber, have been described (Jeffery et al. 2012; Hempel et al. 2014; Zhang et al. 2014). These combinatory types of plastids exhibit multiple functions (Zhang et al. 2014).

In summary, a single amyloplast can harbor numerous starch granules, with its envelope degrading only once the amyloplast becomes full of starch. The quantity of plastid DNA copies per amyloplast is variable and undergoes changes over time. Certain functions associated with starch accumulation appear to necessitate proteins encoded by the plastid genome. Moreover, amyloplasts play roles in various metabolic processes beyond starch production and accumulation. Unlike other plastid types, amyloplasts may coexist with other plastid types, such as chloroplasts or chromoplasts.

## Amyloplasts origin from proplastids and other amyloplasts

A study in *Triticum aestivum* L. describes the events of amyloplast formation from proplastids in the coenocytic endosperm of immature caryopses. During the first week of caryopsis development, the sub-aleurone cells already show amyloplasts with a single-size class of starch granules (A-type starch granules). At 10–12 days after anthesis (DAAs) both the sub-aleurone and the central endosperm cells show protrusions in the amyloplasts and some of these protrusions contain small starch granules (B-type starch granules). The protrusions extend throughout the cytoplasm, sometimes are branched, and become numerous at 17 DAA. A few days later, a third-size class of starch granules (small C-type granules) appear in the cytoplasm (Bechtel and Wilson 2003).

According to other authors, the large amyloplasts coming from proplastids divide and increase in number through binary fission, whereas the small amyloplasts divide and increase in number through the envelope protrusions of the large amyloplasts. The latter amyloplasts show double membranes as the larger ones, but form more than one spherical B-type starch granule, and, after 18 DAAs, clusters of irregular C-type granules (Wei et al. 2010).

The amyloplast fulfills its function when it is full of starch granules. When its envelope begins to degrade, starch granules are released into the cytoplasm. The envelope degradation is highly asynchronous in each amyloplast with some envelope regions remaining intact for some time (Wei et al. 2010).

In contrast to the binary fission of chloroplasts, in which the division machinery controls the size of the organelle (Miyagishima 2011), the amyloplasts may also divide at multiple sites simultaneously without any control in size, as occurs in *Oryza sativa* L. endosperm (Yun and Kawagoe 2009). In the same plant, septum-like structures exist also between starch granules during the formation of the compound starch grains (Yun and Kawagoe 2010), with the formation of septa promoting the compound grain formation (Matsushima et al. 2014).

In summary, there plants in which amyloplasts of different dimension and division mechanisms exhist. In these plants, large amyloplasts come from proplastids and divide through binary fission, whereas small amyloplasts divide through the envelope protrusions of the large amyloplasts. Amyloplast fulfills its function when is full of starch granules. Amyloplasts may also divide at multiple sites simultaneously without any control in size.

## Amyloplast starch activity

Starch consists of two major components; amylose, a linear α-1,4 linked D-glucose polymer, and amylopectin, a branched α-1,4 and α-1,6 D-glucose polymer. As starch deposition progresses, the grain enlarges until it occupies most of the amyloplast interior.

Starch biosynthesis involves the action of numerous enzymes, including ADP-glucose pyrophosphorylase, starch synthases, granule-bound starch synthase (GBSS), starch branching enzymes (SBE), and debranching enzymes (Ma et al. 2018). Starch synthases and SBEs are related to amylopectin synthesis, whereas amylose synthesis is controlled by GBSS (Vrinten and Nakamura 2000).

Membrane transporters serve as exchange components in the amyloplast (Fischer and Weber 2002). It has been suggested that the transport machinery of the amyloplast envelope is complex, and that transport varies with organ type, developmental phase and species. The analysis of the transporters also shows that there are one or more biochemical processes in amyloplast stroma for controlling carbon flux into starch (Cakir et al. 2016).

In the amyloplasts, starch granules also include various lipids (Gayral et al. 2019). In addition to the lipids associated with the inner and outer envelope membranes, some lipids

are also embedded in the starch granules. The presence of lipids within starch granules is specific to cereal endosperm, with lysophospholipids, and especially lysophosphatidylcholine and free FAs, as the main components (Gayral et al. 2019). Regarding the role of these lipids, a close relationship between the accumulation of the starch lipids and amylose has been established (Pérez and Bertoft 2010), and it has been suggested that starch lipids significantly impact starch crystallinity in the caryopses of cereals (Putseys et al. 2010). In plant cells, the synthesis of the galactolipids MGDG and DGDG follows two pathways, one in the plastid (the prokaryotic pathway) and the other in the ER (the eukaryotic pathway). Due to the specificity of the acyltransferases, the MGDG and DGDG produced by the prokaryotic pathway carry C16 FAs at the second acyl (sn-2) position, whereas those produced by the eukaryotic pathway carry only C18 FAs at the same position (Ohlrogge and Browse 1995). Therefore, plants with high levels of C16 in the two lipids are called 16:3 plants, whereas those containing a large amount of 18:3 FAs, are called 18:3 plants. In the former, the two pathways act together, whereas in the latter the eukaryotic pathway is prevalent, but there are possible differences in the interaction between the pathways in different species (Li et al. 2016; Gu et al. 2017, and other references therein). Interestingly, the amyloplasts of *Brassica oleracea* L. buds (a 16:3 plant) and of *Acer pseudoplatanus* L. cells (an 18:3 plant) exhibit comparable lipid compositions of the envelope membrane between chloroplast and amyloplast, suggesting a similar lipid metabolism (Journet and Douce 1985; Alban et al. 1989). By contrast, in *Zea mays* L. (another 18:3 plant), amyloplast and chloroplast membrane lipids show a different FAs composition, because amyloplast galactolipids are mainly composed of linoleic acid (18:2), whereas those of chloroplasts are mainly composed of linolenic acid (18:3) (Tremolieres et al. 1994; Gayral et al. 2015; Gu et al. 2017).

Differently from cereals, lipids are absent in starch granules of amyloplasts of *Solanum tuberosum* L. tubers and cotyledons of dicot seeds (Pérez and Bertoft 2010).

Synthesizing, starch consists of two major components, amylose and amylopectin. It can occupy most of the amyloplast interior. Biochemical processes within the amyloplast stroma regulate the flow of carbon into starch. The transport system of the amyloplast envelope is intricate, and its functionality varies depending on the organ type, developmental stage, and species. In the amyloplasts, starch granules also include various lipids. Differently from cereals, the absence of lipids within starch granules of amyloplasts occurs in *Solanum tuberosum* L. tubers and cotyledons of dicot seeds.

## Amyloplast-to-chloroplast transition and *vice versa*

Amyloplasts and chloroplasts are closely related organelles, not only because both synthesize starch, but also because the amyloplasts contain photosynthesis-related proteins as the chloroplasts. In accordance, many starch metabolism-related proteins exist in both chloroplasts and amyloplasts, suggesting the same conserved pathway of starch metabolism in the two organelles (Liu et al. 2022). The natural consequence of this similarity is that amyloplasts can turn into chloroplasts, e.g. in potato under light (Figure 2(K)) (Anstis and Northcote 1973), and chloroplasts into amyloplasts, e.g. in *Solanum lycopersicum* L. cotyledons cultured *in vitro* in the presence of sucrose (Figure 4(A,B)) (Branca et al. 1994).

However, there are also differences between the two organelles because, for example in *Oryza sativa* L. plants, while the grain amyloplast and the leaf chloroplast DNA sequences are identical, they are differentially methylated, with the chloroplast plastome showing a higher methylation level. These differential methylation patterns are primarily observed in the plastome-encoded genes related to photosynthesis, followed by those involved in transcription and translation (Muniandy et al. 2019), and may have epigenetic consequences on plastid interconversion.

The development of chloroplasts from amyloplasts occurs in roots, storage tissues and some calli. It has been studied in detail in *Solanum tuberosum* L. tuber. In the amyloplast-to-chloroplast transition process in light-exposed tubers, the grana directly derive from vesicles or membranous tubular extensions arising from invaginations of the inner membrane of the amyloplast (Anstis and Northcote 1973). This event is rapidly followed by the accumulation of chlorophyll a and chlorophyll b, which continues for three weeks and is associated with the synthesis of galactolipids (Anstis and Northcote 1973). The light-induced greening usually occurs in the cortical parenchyma 0–1.5 mm below the periderm (Figure 2(K)), involving about ten cell layers (Zhang et al. 2020), and the inception of granum lamellae begins around amyloplasts with a diameter of 9–30 µm (Anstis and Northcote 1973; Petermann and Morris 1985). The transition of the amyloplast to chloroplast is concomitant with the accumulation of glycoalkaloids (Friedman et al. 1997), however, glycoalkaloid synthesis and accumulation in tubers occur via a metabolic pathway independent of that responsible for the production of photosynthetic pigments associated with tuber greening (Tanios et al. 2018).

Potato amyloplasts have different sizes, approximately 5–80 µm in diameter (Muraja-Fras et al. 1994; Miranda and Aguilera 2006), whereas chloroplasts are only 5–10 µm in diameter (Trunova et al. 2003; Sun et al. 2011). Only the small amyloplasts have been reported to be transformed into chloroplasts (Zhu et al. 1984) during the greening process. However, further results suggest that the transformation process is only faster in the smaller amyloplasts (Muraja-Fras et al. 1994; Zhang et al. 2020).

The amyloplast–to-chloroplast transition in tuber tissues of *Solanum tuberosum* L. also includes the formation of a membrane capsule between the plastid envelope and the starch granules (Zhu et al. 1984; Muraja-Fras et al. 1994; Ljubičić et al. 1998). This appears before the differentiation of thylakoids and accumulation of chlorophyll on the newly synthesized membranes. After light-induced greening, the amyloplast membrane disappears in *Solanum tuberosum* L. tuber cells, while grana occur at the periphery of the amyloplast. Then many granum lamellae and osmiophilic bodies are formed and starch is completely dissolved (Zhang et al. 2020). During greening, various stages of chloro-amyloplasts

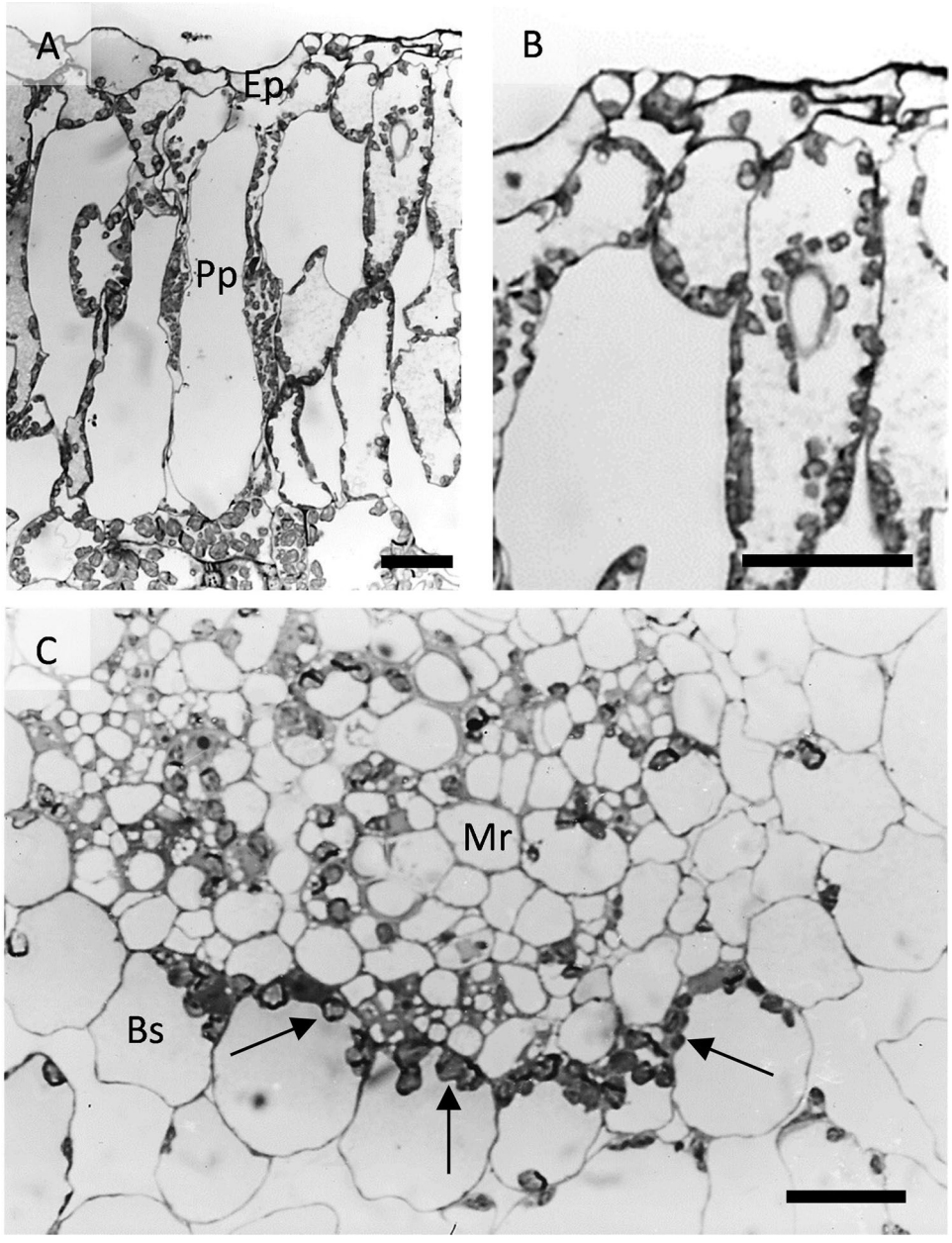


**Figure 4.** (A–C) Transections under light microscopy of *Solanum lycopersicum* L. cotyledons excised from 7-days-old seedlings plated on Murashige and Skoog (1962) medium, containing 0.8% agar and 30 g/1 sucrose, and incubated at 25 °C under a 16h photoperiod. (A) Amyloplasts instead of chloroplasts in the cells of the palisade layers. (B) Detail of a showing amyloplasts at higher magnification. (C) Midrib (Mr) surrounded by a bundle sheath (Bs) with cells filled with mature amyloplasts (arrows). Semithin sections (0.5 µm) stained with toluidine blue and observed with a zeiss axioskope. Unpublished images from Branca et al. (1994). Bs: bundle sheath; E: epidermis; Mr: midrib; Pp: palisade parenchyma. Bars = 30µm.

are also observed and these organelles have been shown to divide in order to give rise to chloroplasts (Ljubičić et al. 1998, and references therein). The rate of conversion of amyloplasts to chloroplasts varies depending on light quality and intensity, the *Solanum tuberosum* L. variety, tuber physiological age, temperature, and atmospheric oxygen levels. The chlorophyll produced in tubers appears stable, because when tubers are exposed to a few days of darkness after greening, chlorophyll degrades very slowly (Virgin and Sundqvist 1992; and other references on Tanios et al. 2018).

During leaf and cotyledon development of *Oryza sativa* L. and *Solanum lycopersicum* L., and other $C_3$ plants with bundle sheaths, starch is accumulated in the immature chloroplasts of both mesophyll and bundle sheath cells, with higher levels in the latter (Miyake 2016). These immature chloroplasts have amyloplast-like profiles and may be considered chloro-amyloplasts. During leaf maturation they may develop into mature chloroplasts (Miyake 2016). However, the opposite is also possible, because at least those of the bundle sheath may become mature amyloplasts, as occurs in sucrose-cultured tomato cotyledons (Figure 4(B)) (Branca et al. 1994). Similarly, detached *Oryza sativa* L. leaf blades placed in distilled water under illumination show bundle sheath plastids accumulating large amounts of starch. It has been suggested that the starch-accumulating activity of the bundle sheath cells of $C_3$ plants might be a possible pre-condition for the evolution of $C_4$ photosynthesis, alternatively, the accumulated starch grains may function as statoliths (Miyake 2016).

In summary, the amyloplasts contain photosynthesis-related proteins and many starch metabolism-related proteins in common with chloroplasts. The natural consequence of this similarity is that amyloplasts can turn into chloroplasts and *vice versa*. The development of chloroplasts from amyloplasts has been observed in roots, storage tissues and some calli of some species, where occurs concomitantly with the accumulation of glycoalkaloids. Amyloplast and chloroplast DNA sequences are identical, but differentially methylated. Methylation may have epigenetic consequences on the plastid interconversion. During greening in *Solanum tuberosum* L. tuber cells, various stages of chloro-amyloplasts are observed and give rise by division to chloroplasts with a conversion rate depending on light quality and intensity.

## *Amyloplasts as statoliths*

In addition to their prevalent storage function, amyloplasts also contribute to gravitropism signaling (Nakamura et al. 2019, and references therein). For example, amyloplasts with large starch granules, known as statoliths, are present in the columella of the calyptra at the root tip where they are essential for the gravitropic response (Hou et al. 2016; Zhang et al. 2019; Levernier et al. 2021) and are differentiated early during root development (Figure 2(L,M)). Amyloplasts sensing gravity are also found in the endodermal cell layer of the shoot, and possibly in the bundle sheath cells of the leaves of some species (Sack 1991; Miyake 2016).

During the sensing process, shoots and roots perceive directional information for gravity at specialized sensing cells named statocytes giving rise to negative and positive gravitropism responses, respectively. Statocytes utilize statoliths to fulfill this function (Figure 2(N)).

Only a few factors responsible for the gravity signaling process have been identified in the statocytes after amyloplast sedimentation (Boonsirichai et al. 2002; Morita 2010).

The TOC complex has been shown to act in the translocation and insertion of plastid-targeted proteins across and into the outer-envelope membranes of the amyloplast (Lee et al. 2018).

Under steady-state conditions, amyloplasts functioning as statoliths are positioned at the bottom of the statocytes. Upon reorientation of the plant organ in response to gravity, the amyloplasts sediment to the new bottom side of these cells with this repositioning converted into a biochemical signal which regulates the directional transport of auxin. Upon reorientation in both root columella cells and hypocotyl endodermal cells, the auxin efflux carrier PIN-FORMED 3 re-localizes to the bottom side of the cells (Friml et al. 2002; Harrison and Masson 2008; Kleine-Vehn et al. 2010; Rakusová et al. 2011), resulting in a directional transport of auxin towards the lower side of the reoriented organs. Thus, auxin is the hormone that is directionally transmitted from the statocytes to the cells of the neighboring tissues, causing differences in the rates of cell growth between the upper and lower flanks of the organ in response to gravity sensing.

In the root tip, the internal part of the root cap (the calyptra) contains sedimented amyloplasts (Figure 2(N)) and the removal of the root cap prevents root gravitropism (Juniper et al. 1966; Tsugeki and Fedoroff 1999; Wang et al. 2005). In *Arabidopsis thaliana* (L.) Heynh shoots, sedimented amyloplasts are found in the stem endodermal layer (Sack 1991), and mutants lacking an endodermis show a complete loss of shoot gravitropism (Fukaki et al. 1998).

Thus, both columella and shoot endodermal cells commonly function in gravity sensing in the respective organs through sedimented amyloplasts, however with morphological differences between the two. True amyloplasts according to the orthotypical definition of these plastids are found in the root columella cells (Sack 1991). In contrast, the amyloplasts of the shoot endodermis have a developed thylakoid membrane system with photosynthetic pigments in addition to well-developed starch granules (Morita 2010) and can be classified as chloro-amyloplasts with both photosynthesis and gravity sensing functions. The common statolith function of both root columella amyloplasts and shoot endodermal chloro-amyloplasts has been supported by the observation that *Arabidopsis thaliana* (L.) Heynh mutants lacking the ability to synthesize starch do not exhibit amyloplast sedimentation and show reduced gravitropic response in both roots and shoots (Caspar and Pickard 1989; Kiss et al. 1989, 1996, 1997; Weise and Kiss 1999).

The motion of the statoliths in the statocytes is closely associated with actin filament action (Collings et al. 2001, Morita 2010). Indeed, the disruption of the actin filaments by treatment with latrunculin B, an inhibitor of actin polymerization, may result in reduction of amyloplast motion (Saito et al. 2005), even though contrasting results have been also obtained, e.g. in *Arabidopsis thaliana* (L.) Heynh and *Zea mays* L. (Morita 2010, and references therein).

More recent data show that the loss of function of DISTORTED1 (DIS1)/ACTIN-RELATED PROTEIN3 (ARP3) in *Arabidopsis thaliana* (L.) Heynh alters actin organization, leading to the formation of abnormally thick actin bundles around the amyloplasts. These strong bundles cause an insufficient sedimentation of amyloplasts in the direction of gravity and a defective root gravitropic response, both restored by latrunculin B treatment (Zheng et al. 2015; Zou et al. 2016). In addition, the loss of RICE MORPHOLOGY DETERMINANT function causes the reduction of the ring-like structure of actin filaments around the amyloplasts favoring their faster sedimentation in the direction of gravity (Huang et al. 2018). A possible mechanistic explanation has been proposed via the characterization of *Arabidopsis thaliana* (L.) Heynh SHOOT GRAVITROPISM9 (SGR9), an amyloplast-localized E3 ubiquitin ligase, because mutations in this protein lead to defective shoot gravitropism (Nakamura et al. 2011; Morita and Nakamura 2012). Loss of SGR9 leads to an increased association between amyloplasts and actin filaments, resulting in a random directional movement of the amyloplasts in the mutant, causing a significant reduction in amyloplast sedimentation. Thus, SGR9 might modulate the dynamics between amyloplasts and actin filaments, enabling the organelles to sediment in the direction of gravity (Nakamura et al. 2019).

Many researchers have proposed that stretch-activated $Ca^{2+}$ channels localized to the plasma membrane of the

statocytes act as putative gravity sensors, activated by the physical force generated by amyloplast sedimentation, possibly *via* actin filaments (Perbal and Driss-Ecole 2003). These activated $Ca^{2+}$ channels are assumed to consequently increase the concentration of $Ca^{2+}$, which might be the signaling molecule transducing the information derived from the sedimentation of statoliths within the statocytes (Nakamura et al. 2019). In addition, a role for the vacuole cannot be excluded.

In *Arabidopsis thaliana* (L.) Heynh shoot endodermal cells, amyloplasts are enclosed by the vacuolar membrane, which influences their movement by its plasticity. Consistent with this, several *sgr* mutants are also defective in vacuole genesis (Hashiguchi et al. 2014; Nakamura et al. 2019, and other references therein). In accordance, one of the SGR proteins (SHOOT GRAVITROPISM6) is involved in the formation and plasticity of the tonoplast of the shoot endodermal cells (Hashiguchi et al. 2014), but also in the amyloplast motion. In fact, the loss of its function causes severe defects in tonoplast ability to change morphology, and this is coupled with a reduced motion of the amyloplasts (Hashiguchi et al. 2014; Nakamura et al. 2019).

In conclusion, both the columella cells of the root cap and shoot endodermal cells function as positive and negative, respectively, gravity sensors through sedimented amyloplasts (statoliths), however with morphological differences between the two. True amyloplasts are found in the root columella cells, whereas the amyloplasts of the shoot endodermis can be classified as chloro-amyloplasts because they have a developed thylakoid membrane system with photosynthetic pigments in addition to well-developed starch granules. Auxin is the hormone that is directionally transmitted from the cells containing the statoliths, named statocytes, to the cells of the neighboring tissues, causing differences in the rates of cell growth between the upper and lower flanks of the organ in response to gravity sensing. Numerous researchers have suggested that stretch activated $Ca^{2+}$ channels located in the plasma membrane of statocytes serve as potential gravity sensors. These channels are hypothesized to be activated by the mechanical force induced by amyloplast sedimentation, potentially facilitated by actin filaments.

## Origin, dynamics and death of gerontoplasts

The transition from chloroplast to gerontoplast has been studied in developing seeds, e.g. in the inner integument cells of *Jatropha curcas* L. seeds (Shah et al. 2016) and in senescent leaves (Figures 1(H) and 2(G)) (Mulisch and Krupinska 2013). The similarity between seeds and leaves concerns the dismantling of the internal membrane system, stroma degradation and formation of stromule-derived vesicles (Shah et al. 2016).

Gerontoplasts appear only in senescent cells as a result of chloroplast aging and are unable to multiply, except for redifferentiation, which occurs only at early developmental stages when they might revert to chloroplasts by the process known as rejuvenation (Zavaleta-Mancera et al. 1999a, 1999b). In these cases, the species-specific retention of the plastome is crucial for determining the gerontoplast-to-chloroplast transition. In fact, after plastome degradation, the fate of the gerontoplast is finally determined and cannot be rejuvenated.

Chloroplasts undergo alterations already at the very beginning of senescence. However, they remain the last organelles to collapse during this developmental process (Lim et al. 2007). The most characteristic morphological features of the transition from chloroplast to gerontoplast are volume alterations, changes from ellipsoid to circular organelle morphology, and deep reorganization of the internal membranes. In accordance, Mulisch and Krupinska (2013) identified three stages as the most relevant ultrastructural changes associated with the transition of a mature chloroplast into a gerontoplast, i.e. breakdown of the thylakoid membrane system, increase in size and number of PGs, and alteration and disruption of the plastid envelope. Several senescence-associated genes function to catalyze the catabolic events involved in this transition. For example, the regulatory network transition from chloroplast to gerontoplast involves the NAC and WRKY transcription factor families that regulate the expression of *Senescence-Associated Genes* (*SAGs*) (Woo et al. 2019). The disorganization of the internal membrane network of the chloroplast is characterized by grana unstacking, flattening of thylakoids, swelling of intra-thylakoid space, and degradation of stroma lamellae.

Multiple variants during the progress of senescence can occur depending on plant genotype, environmental conditions, and stress factors (Mulisch and Krupinska 2013). An anomalous breakdown of the thylakoid system may result from the formation of dilations at the thylakoid ends, cup-shape stacked membranes, and thylakoid coiling (Wrischer et al. 2009). However, the structural changes characteristic of gerontoplasts also include a macromolecular reorganization of thylakoid protein complexes. The initial phase of this rearrangement involves the stacking of grana, which relies on the mutual interactions between PSII–LHCII supercomplexes situated on facing thylakoid membranes (Albanese et al. 2020). The dismantling of this supercomplex is followed by the breakdown of chlorophyll and the degradation of the LHCII, events preceding the grana unstacking (Domínguez and Cejudo 2021).

Chlorophyll cleavage is a multi-step process involving the reduction of chlorophyll b to chlorophyll a, the removal of the central Mg atom of chlorophyll a, generating pheophytin a (Shimoda et al. 2016), the elimination of the phytol chain of pheophytin a (Schelbert et al. 2009), the formation of non-phototoxic blue-fluorescent and red chlorophyll catabolites (Pruzinská et al. 2003, 2007).

After chlorophyll cleavage, the disintegration of the PSII–LHCII supercomplex occurs as a prerequisite for the separate degradation of PSII and LHCII complexes. In contrast with PSII, PSI and ATPase complex activities seem to be stable until the final phases of leaf senescence, declining sharply thereafter with the degradation of the proteins of the PSI core and reaction center, and the LHCI complex (Prakash et al. 2001; Guiamét et al. 2002; Krupinska et al. 2012; Nath et al. 2013). In accordance, in plants, such as *Spinacia oleracea* L., *Nicotiana tabacum* L., or *Arabidopsis thaliana* (L.) Heynh, the formation of PSI–LHCII supercomplexes is also observed in senescing chloroplasts (Schwarz et al. 2018). Although the chloroplast

photochemical machinery and the linear electron transport chain are dismantled during senescence, gerontoplasts undergo additional macromolecular rearrangements allowing alternative electron transport pathways that preserve the production of ATP, necessary for supporting the highly energy demanding processes (Krieger-Liszkay et al. 2019).

Grana stacking and unstacking is a reversible process, and its dynamics depends on the increase of membrane fluidity, thylakoid lumen expansion, and enlargement of the junctional slits between adjacent thylakoids. Phosphorylation, oligomerization, and thylakoid curvature-induced movements at grana margins depend on the activities of the CURVATURE THYLAKOID1 proteins (Armbruster et al. 2013; Pribil et al. 2018; Trotta et al. 2019).

Chlorophyll and thylakoid membranes dismantling release large amounts of FAs and phytol. Two enzymes, located in the PGs, phytyl ester synthase 1 and 2, are involved in sequestering these catabolic products in TAG and FA-phytyl ester, which contribute to the formation of giant PGs. The carotenoids remaining in the gerontoplasts are degraded by Carotenoid Cleavage Dioxygenase 4 (CCD4). Thus, the transition from chloroplast to gerontoplast occurs in close relationship with PGs, which play a dual role by storing catabolic products and participating in their release and conversion into storage compounds (Rottet et al. 2015).

During senescence, chloroplast double-membrane envelopes typically undergo changes and alterations, such as perforations and ruptures (Springer et al. 2016) and stromule formation (Ishida et al. 2008).

Due to their structural function as constituents of the membrane network of the chloroplast, lipids are critical for chloroplast dismantling. The enzyme 13-lipoxygenase, which is localized at the plastid envelope, catalyzes the dioxygenation of unsaturated membrane FAs, thereby facilitating the disruption of the envelope, thus allowing the release of stromal components (Springer et al. 2016). Being the major lipid components of thylakoid membranes and crucial players in the structure and stability of photosynthetic complexes, the galactolipids MGDG and DGDG are the main targets of chloroplast degradation (Webb and Green 1991; Hölzl and Dörmann 2019).

Phytol released from pheophytin and FAs resulting from the degradation of the galactolipids of the thylakoid membranes accumulate inside PGs of the differentiating gerontoplasts, thereby avoiding their toxicity (Besagni and Kessler 2013; Rottet et al. 2015). In PGs, FAs and phytol are converted to FA-phytyl esters, tocopherol and triacylglycerol and as stated above, the carotenoid degradation occurs via CCD4 activity (Ytterberg et al. 2006; Lundquist et al. 2012; Rottet et al. 2016).

Leaf senescence is a developmental program modulated by various signals, including ROS. Chloroplasts are an important source of ROS in photosynthesis but are also targets of ROS-triggered damage. The thiol-dependent antioxidant and redox regulatory systems are functionally interconnected and affect chloroplast stability in senescing leaves (Cejudo et al. 2021). *Arabidopsis thaliana* (L.) Heynh mutants severely impaired in chloroplast redox homeostasis show bleaching of cotyledons, which are characterized by chloroplasts with the structural features of gerontoplasts (Ojeda, Nájera, et al. 2017; Ojeda, Pérez-Ruiz, et al. 2017).

SOUL4 is a PG protein with heme-binding activity (Shanmugabalaji et al. 2020). Since heme accumulation may increase ROS production, the heme-binding activity of SOUL4 suggests an additional role for PGs in controlling the chloroplast pool of heme groups, hence avoiding potential harmful effects of ROS production by these groups during the transition from chloroplast to gerontoplast. However, various degradation by-products resulting from chloroplast breakdown may be toxic; hence, the transition process must be tightly regulated, as suggested by Zentgraf and co-workers (Zentgraf et al. 2022).

The degradation of stroma proteins involves a combination of intra-plastid and extra-plastid processes. For example, the degradation of Rubisco is initiated inside the chloroplast (Feller et al. 2008; Lee et al. 2013) but is completed by extraplastid degradation pathways (Lee et al. 2013). Moreover, the reduction in chloroplast stromal proteins, including Rubisco, typically precedes the decline in chloroplast number, as in *Triticum aestivum* L., *Hordeum vulgare* L., and *Arabidopsis thaliana* (L.) Heynh (Martinoia et al.1983; Mae et al. 1984; Ono et al. 1995; Wada et al. 2009). The degradation of stroma proteins during senescence allows the reutilization of their amino acids as a source of nitrogen in sink tissues. Rubisco contributes up to 50% of the soluble proteins and up to 30% of the total leaf nitrogen in $C_3$ plants, thus being a key protein to ensure nutrient mobilization (Feller et al. 2008). Besides various types of proteases that act inside the senescing chloroplast, extra-plastid pathways also mediate the degradation of this organelle proteins. An intensive formation of different vesicles can be observed, ranging from Rubisco-containing bodies (RCBs) to senescence-associated vacuoles and chloroplast vesiculation-containing vesicles (Izumi and Nakamura 2018; Domínguez and Cejudo 2021). Moreover, also whole chloroplasts can be degraded by the process known as chlorophagy (Zhuang and Jiang 2019) or by the 26S proteasome mediated by a cytosol localized E3 ubiquitin ligase (Woodson et al. 2015). However, the degradation processes inside and outside the chloroplasts must be coordinated and different pathways are induced at distinct time points during leaf senescence (Zentgraf et al. 2022).

In summary, gerontoplasts appear in senescent cells as a result of chloroplast aging. They are unable to multiply, except for redifferentiation, which occurs only at early developmental stages when they might revert to chloroplasts in the process known as rejuvenation. Gerontoplast-to-chloroplast transition is species-specific and involves the retention of the chloroplast plastome. In fact, after plastome degradation, the fate of the gerontoplast is determined and it cannot be rejuvenated. The most relevant ultrastructural changes associated with the transition of chloroplast into gerontoplast are the breakdown of the thylakoid membrane system, the increase in size and number of PGs, and the alteration and disruption of the plastid envelope. Several senescence associated genes catalyze the catabolic events involved in this transition. Multiple variants during the progress of senescence can occur depending on plant genotype, environmental conditions, and stress factors. Even if the

chloroplast photochemical machinery and the linear electron transport chain are dismantled during senescence, gerontoplasts undergo macromolecular rearrangements allowing alternative electron transport pathways that preserve the production of ATP, necessary for attending the highly energy demanding processes. The galactolipids MGDG and DGDG are targets of chloroplast degradation. Phytol released by pheophytin and FAs resulting from the degradation of these galactolipids accumulate inside the PGs of the differentiating gerontoplasts. Senescence is a developmental program modulated by various signals, including ROS. Besides various types of proteases act inside the senescing chloroplast, also extra-plastid pathways mediate the degradation of its proteins. Moreover, whole chloroplasts can be also degraded by the process known as chlorophagy, described below.

## *Chlorophagy*

In plant cells, both macroautophagy and microautophagy pathways contribute to chloroplast degradation, and exhibit cargo specificity under different conditions, e.g. during leaf senescence (Xie et al. 2015; Izumi and Nakamura 2018; Nakamura and Izumi 2018; Otegui 2018; Soto-Burgos et al. 2018). The macroautophagy process utilizes the formation of autophagosomal structures (Figure 5) and requires proteins coded by Autophagy Genes (ATGs) (Wada et al. 2009), such as ATG8 (Zhuang et al. 2013; Spitzer et al. 2015; Zhuang et al. 2017; Zhuang et al. 2018; Yagyu and Yoshimoto 2024). An example of macroautophagy-related structures occurs during sugar starvation in whole darkened plants. These structures are small spherical bodies (around 1 µm) surrounded by autophagosome-like double membranes, named Rubisco-containing bodies (RCBs) (Figure 5) (Ishida et al. 2008), and small starch granule-like structures (SSGLs) (Wang et al. 2013a).

The detection of Rubisco in RCBs was first observed in both the cytoplasm and vacuole of *Triticum aestivum* L. leaves (Chiba et al. 2003). The RCB formation is strictly associated with the extending stromules (Zhuang and Jiang 2019), which participate in their formation and release (Ishida et al. 2008), as in the case of SSGLs (Wang et al. 2013b). Macrochlorophagy by RCBs is considered an indirect vacuole-invagination process (Figure 5).

In comparison to macroautophagy, microautophagy always mediates chloroplast degradation by its direct invagination *via* the vacuole membrane (Figure 5). When the chloroplast becomes abnormally swollen/shrunken by the overexpression of vesicle inducing protein in PLASTID1, a protein that regulates chloroplast envelope integrity (Nakamura et al. 2018), recognition by the ATG8-containing structures and of the chlorophagy receptors occurs and is followed by vacuolar invagination (Yagyu and Yoshimoto 2024).

Alternatively, the formation of ATG8-sac structures could promote the establishment of cap-like formations on the chloroplast, thus regulating the attachment and merging of the chloroplast membrane with the tonoplast, subsequently leading to the release of the chloroplast into the vacuolar lumen (Zhuang and Jiang 2019). Examples of whole organelle chlorophagy are given by leaves undergoing senescence induced by dark (Wada et al. 2009) or UV-B/high visible light, which acts as a photodamaging radiation (Figure 5) (Izumi et al. 2017). In such circumstances, large and abnormal autophagosomes, exceeding a length of 1 µm, emerge to encapsulate impaired chloroplasts by the activity of the chloroplast vesiculation (CV) plastid-targeted protein involved in their specific direct transport to the vacuole (Wang and Blumwald 2014; Domínguez and Cejudo 2021). In *Arabidopsis thaliana* (L.) Heynh, expression of the *CV-GFP* construct causes the formation of chloroplast-derived vesicles of about 1 µm in diameter referred to as CV-containing vesicles containing stroma,

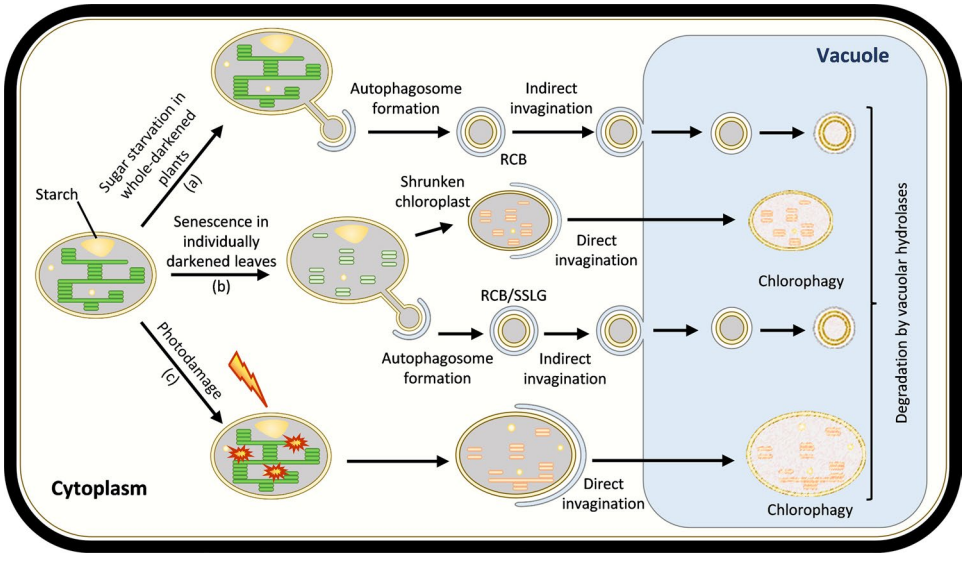


**Figure 5.** Diagram showing the main types of chlorophagy mechanisms. (a) Under nutrient starvation conditions (e.g. carbon or nitrogen deficiency), macroautophagy occurs via rubisco-containing bodies (RCBs) induced in whole-darkened plants. RCBs contain stromal proteins, including rubisco subunits and are produced via stromule formation. (b) As darkened individual leaves undergo accelerated senescence, chloroplast shrinkage occurs, and entire chloroplasts are transported into the vacuole via direct invagination (microautophagy). Alternatively, a macroautophagic process via RCBs/small starch granule-like structures (SSGLs) can occur. (c) Degradation of the entire chloroplast can be induced by photodamage due to exposure to UV-B, strong visible light, or natural sunlight. Collapsed chloroplasts are transported directly into the vacuole without RCB formation. (adapted from Izumi and Nakamura 2018; Wan and Ling 2022).

envelope, and thylakoid proteins (Wang and Blumwald 2014). These vesicles do not associate either with the autophagosome marker GFP-ATG8a, or with the lytic senescence-associated vacuoles known as SAVs (Izumi and Nakamura 2018). SAVs are characterized by a senescence-induced cysteine protease and seem to represent a separate pathway for chloroplast dismantling in which the *senescence-associated gene 12* (*SAG12*) appears to be involved (Otegui et al. 2005). SAVs display similar characteristics to the lytic vacuole although they lack the tonoplast marker γ-TIP (Otegui et al. 2005). However, they contain stromal proteins including Rubisco and glutamine synthetase, but lack thylakoid proteins (Martínez et al. 2008).

Stromules are important for all types of plastids but are more abundant in senescence-related processes (Brunkard et al. 2015; Caplan et al. 2015). Stromules are active structures that extend along microfilaments of actin and the ER. Their formation is plastid autonomous, in fact stromules can still form on isolated chloroplasts after extraction from the cytoplasm. In addition, plastid-derived vesicles are suggested to bud from stromules through tip shedding or simple breakage, either to recycle plastid content, to remove toxic molecules, or for intracellular communication (Hanson and Hines 2018). Utilizing the stromules, plastids establish direct connections with other subcellular compartments, including the nucleus. The ROS generated in chloroplasts are translocated through these tunnels into adjacent nuclei (Exposito-Rodriguez et al. 2017).

Plastoglobules formed during the chloroplast-senescing program are degraded via intra- and extra-plastid events. A pathway for PG degradation may occur within the chloroplast (Liu 2016), but most PGs are secreted outside the organelle, either by direct exposure at the plastid surface or by protrusion of PG-containing vesicles (van Doorn and Prisa 2014; Liu 2016). When in the cytosol, the PGs or the PG-containing vesicles are swallowed by the central vacuole, where they undergo degradation (Liu 2016). This mechanism is similar to microlipophagy, a process involved in the degradation of lipid droplets during starvation-induced stress (Fan et al. 2019).

As summarized in Figure 5, both macroautophagy and microautophagy pathways contribute to chloroplast degradation. The macroautophagy utilizes the formation of autophagosomal structures and requires proteins coded by Autophagy Genes (ATGs). The macroautophagy-related structures, surrounded by autophagosome-like double membranes, are named RCBs. Macrochlorophagy by RCBs is considered an indirect vacuole-invagination process. Microautophagy mediates the degradation of chloroplast by its direct invagination *via* the vacuole membrane. Examples of whole organelle chlorophagy are given by leaves undergoing senescence induced by dark or UV-B/high visible light. In such circumstances, large and abnormal autophagosomes emerge to encapsulate impaired chloroplasts by the activity of the CV plastid-targeted protein, which is involved in their direct transport to the vacuole. Stromules are abundant in senescence processes. Their formation is plastid autonomous, and they are utilized to establish direct connections with other subcellular compartments. Plastoglobules formed during the chloroplast-senescing program are degraded via intra- and extra- plastid events. When out of the plastid, they are swallowed by the central vacuole, where undergo degradation.

## Outlooks

The ideas for further investigation that the review provides are many, but some of them arouse our particular interest.

The transition dynamics among the functional and morphological features of the plastid types show that plastid differentiation is not definitive, except for gerontoplasts. This is a first point needing further investigation. Gerontoplasts are usually present in senescing leaves, however it is known that plants are either deciduous or evergreen. In the first ones, gerontoplasts differentiate at about the same time in all the leaves, whereas it is not the case of the evergreen plants, where gerontoplast differentiation is an individual-leaf specific event. It is known that numerous phytohormones, e.g. jasmonic acid, abscisic acid, and salicylic acid, work together in leaf senescence, as well as transcription factor families regulating the expression of senescence-associated genes (Domínguez and Cejudo 2021). As shown in this review, the scenario is complex, and involves chlorophagy. However, the black box is still how this multifactorial control is simultaneously transmitted at the same time to the entire leaf system, as occurs in deciduous plants.

This is a point of interest, which deserves more attention in the future both for acquiring a deeper knowledge in basic plant biology and for agriculture implications.

If gerontoplasts are important for their unique (final) fate in plastid differentiation, so are proplastids, but for an opposite reason, i.e. because they are at the beginning of multiple plastid differentiation fates. The present review has shown how specialization within plastid populations aligns with the different cellular properties, and generally derives from proplastids. This proplastid multipotency seems to come from its origin. In angiosperms, the transmission of plastid DNA across generations generally occurs through the egg cytoplasm, because plastid DNA is typically degraded in the pollen. Thus, the potential capabilities of proplastids of male origin remain largely unknown. A recovery of the genetic information coming from male meiosis could be important to broaden our knowledge on proplastid capabilities for differentiation. The biotechnology known as experimental androgenesis may be a way to investigate still unknown aspects of proplastid differentiation. Experimental androgenesis is the *in vitro* production of embryoids of male gametophyte origin. When followed by the production of fertile homozygous double haploid plants, it gives the opportunity to investigate events of male origin (Hale et al. 2021), such as, in our case, the differentiation potentialities of proplastids.

Another topic that requires further study concerns the xyloplasts, as this plastid class has only recently been identified, and for this reason, is still poorly characterized. According to Pinard et al. (2019) their diversity depends on the cell types present in wood and is under developmental control. Again, biotechnology, associated with cryoelectron microscopy, can be useful to deepen knowledge on this plastid type and for the identification of specific plastid proteins. Experimental xylogenesis is the *de novo* production of vascular elements, and associated cells, in the callus produced through *in vitro* culture (Keret et al. 2023). Thus, the production of xyloplasts in xylogenic cells of the callus, and the

possible increase in xyloplast diversity caused by somaclonal variation events (Duta-Cornescu et al. 2023), may extend our knowledge about these plastids and their possible plastidial interconversion.

## Conclusions

Recent and past data show that in land plants the specialized functions of plastids and their interconversion are strictly interdependent and are the expression of the differentiation dynamics of the plant. There are internal positional signals that lead to specific changes in organelle proteome and morphology. There is a strict relationship between plastid plasticity and the dynamics of plant development. Plastids are therefore sensors of plant development and help to explain it. As shown in the Outlook Section there are numerous aspects that still need to be investigated. However, what is still missing is good integration between cytology, molecular biology and genetics data. A comprehensive overview for all plastid types and of their similarities would help to understand their cytological transitions revealing the basis of their plasticity. As also recently suggested by other Authors (Christian et al. 2023), understanding the basis of extreme morpho-functional and metabolic heterogeneity in diverse plastid types will help in identifying mechanisms that will aid in developing climate resilient crops.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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