



# Plastid Structural Adaptations and Functional Diversity: Understanding the Link

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# Abstract

Plastids are significant organelles found commonly in plant and algal cells for photosynthesis and other specialized functions. Chloroplasts are capable of converting light into chemical energy stored in the bonds in glucose using the chlorophyll in thylakoids and other biochemicals in stroma. These plastids are mainly green owing to the presence of chlorophyll found in grana thylakoids. During fruit ripening and other developmental processes there is changeover of chloroplasts to chromoplasts which is characterized by thylakoid degradation accompanied by chlorophyll loss while plastoglobules increase, and carotenoids get accumulated. This irreversible change is common in different vegetables and fruits. On the other hand, change from chloroplasts to gerontoplasts happens with the age therefore changing the structures and general functionality of photosynthesis. Moreover, it has been identified that elaioplasts which are the component part of lipid storage are present in different plant organs such as flowers, fruits as well as seeds. Their development is species specific and has been exemplified by studies in Arabidopsis thaliana which shows that proplastids develop into elaioplasts at a particular stage of development. This article is a systematic and detailed analysis of plastid types, their functions and their conversion, focusing on the importance of functional diversification of plastids, and its relation to plant differentiation and evolution.

KEYWORDS Photosynthesis, Senescence, Lipid biosynthesis, Carotenoids, Glucose.

# 1 | INTRODUCTION

In many plants plastid transmission is uniparental, where most of the angiosperms plastids are inherited from the female gametophyte and many of the gymnosperms 'plastids are inherited from the male gametophyte (Sakamoto & Takami, 2024). Plastids in algae also exhibit the system of uniparental inheritance. In general, intraspecific crosses produce offspring with plastids derived solely from the maternal parent(Choi et al., 2020). Only in a few instances have researchers been able to demonstrate the transfer of plastid DNA from the male parent. As for the possibility of seed transmission, it may be said that plastids are inherited strictly through the female genotype (Sakamoto & Takami, 2024). Only occasionally have researchers observed the transfer of plastid DNA to male progeny While in interspecific hybridizations there can be more irregularity in the flow of plastids

where certain hybrids of flowering plants takes from the male parent (Chung et al., 2023). Interestingly, it has been estimated that of all the angiosperms approximately 20% could be characterized by the totally biparental inheritance of plastids.

With advancement in growth of maize seedlings the plastid DNA becomes sensitive to oxidative damage resulting from photo-oxidative effects and electron transport chain events in photosynthesis and respiration processes. Although some damage can be repaired, if it is not repaired then damages to the DNA can turn into nonfunctional entities (Alghoul et al., 2023). Although, nuclear encoded DNA repair proteins, involved in all the three sub-pathways are transported and act in plastids maintaining genome stability (Zayed et al., 2023). For examples, in nucleus of the moss *Physcomitrella patens*, DNA mismatch repair protein Msh1 binds recombinational repair proteins RecA and RecG to maintain the integrity of the plastid genome (Taylor et al., 2023).

#### Origin

Plastids are derived from endosymbiotic cyanobacteria and the first endosymbiosis happened in Archaeplastida ~1. About 5 billion years ago with the help of which eukaryotes began to carry out photosynthesis (Gruber & Medlin, 2023). This led to the evolution of three lineages, Chloroplasts are found in green algae and plants, while rhodoplasts-marked red algae and muroplasts characterized glaucophytes. These plastids are of different nature in their pigmentation and morphological characteristics, the glaucophytes, for instance have preserved the cyanobacterial cell wall. In Paulinella a new primary endosymbiosis occurred at the age of approximately 90-140 million years that produced the cyanelle, and differs from those of Archaeplastida (Lhee et al., 2024).Secondary endosymbiosis produced complex plastids and eukaryote preved on another eukaryote with a primary plastid and thus formed plastids possessed more than two membranes and usually had lesser functions (Völkner et al., 2024). This type of

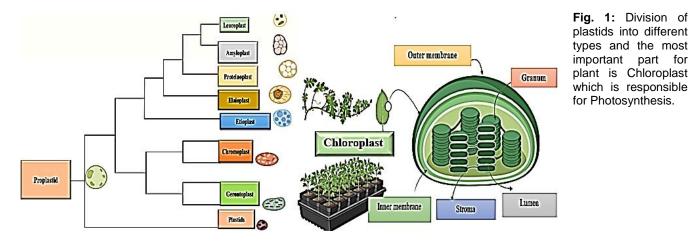
plastids formed through second Endosymbiosis of a red alga are present in the heterokonts, haptophytes, cryptomonads and majority of dinoflagellates rhodoplast. Some of the species that have engulfed a green alga are known as euglenids and chlorarachniophytes or chloroplasts. The 'apicoplast' is no more involved in photosynthesis but is essential organelle and another area where chemicals that can selectively end up in the 'apicoplast' can be produced to treat malaria (Bennett et al., 2024).

#### **Types and Roles of Plastid**

The attributes of each plastid type are closely linked to their distinct functions Table 1 (Fig. 1). Proplastids, also known as undifferentiated plastids, are characterized by their small size and distinct ultrastructure's (Choi et al., 2021). Meristematic and reproductive tissues are mostly found in the plastids. They can be differentiated into different types on the bases of pigments as chromoplasts in either red, orange and yellow, leucoplasts in white, and chloroplasts are in green. Etioplasts are intermediate forms of chloroplasts, and gerontoplasts are senescent forms of the same (Sierra et al., 2023).

 Table 1: represents the genes involved the various plastids types and their role

Genes in the	References		
Chloroplast	psbA	Photosystem II protein D1	(Wang et al., 2023)
	psaA	Photosystem I apoprotein A1	(Yang et al., 2020)
	petB	Cytochrome b6	(Li et al., 2023)
	atpB	ATP synthase subunit	(Chaux et al., 2023)
Etioplasts	ChIB, chIL, chIN	Encoding light independent prtochlorophyllide reductase	(Yamamoto et al., 2020)
Chromoplast	Psy	Phytoene synthase	(Gupta et al., 2022)
	Pds	Phytoene desaturase	(Gupta et al., 2022)
	Zds	ζ-carotene desaturase	(Wang et al., 2020)
	lcyB	Lycopene β-cyclase	(Zhao et al., 2020)
Amyloplast	Sps	sucrose-phosphate synthase	(Fünfgeld et al., 2022)
	Adg1	ADP-glucose pyro phosphorylase	(Fünfgeld et al., 2022)
	gbss1	granule-bound starch synthase	(Seung, 2020)
	psa, psb, pet and ndh	Encode Photosystem I, II, cytochrome b6f	(Tikhonov, 2014)



#### Proplastids

Proplastids are considered as the least developed plastids that have little or no sign of structural system. Thus, that their organelle transmission can occur from one generation to the other (Skrzypkowski & Kiełkowska, 2024). They are colourless and almost microscopic in comparison with the other type of plastid, the lack of a distinctive shape(Srivastava et al., 2024). They are mostly reported in meristematic, egg cells of the plants and sometimes occurs during the pollen formation in certain species like Pelagonium and *Hordeum vulgare*. Furthermore, the nodule proplastids in root tissues were identified to have a central role in the biochemical pathway of nitrogen fixation in the family of legumes (Gruber & Medlin, 2023).

#### Chloroplasts

Among photosynthetic species, chloroplasts are common (Fig. 2) and one of the most researched plastid types (Kuntz et al., 2024).Chloroplasts are one of the

kinds of plastids that are found in the photosynthetic organisms they help in trapping light energy and transforming that energy into chemical energy (Zhang et al., 2024). They bear thylakoids which are disc shaped structures that aggregate to form the granule, thus offering a large surface area for the photosynthetic protein particles (Lazzarin, 2023). Carotenoids are accumulated by plastoglobules, which are hydrophobic structures localized at the thylakoid edges and play a role in carotenoid metabolism other than endogenous carotenoids. Apart from chlorophyll, chloroplasts contain such terpenes as lutein, *β*-carotene, and xanthophylls which are involved in photosynthesis and are most important for the prevention of photo damage (Chauhan et al., 2023). For examples, xanthophylls assist in the eliminate of the overheated energy of light and clean up the ROS thus fine the photosynthesis and ROS processes (Ji et al., 2023). This makes them involved in energy harvesting and also compartment for protection and making their meals of starch, proteins and lipids when the cellular needs are under different circumstances (Roca et al., 2024).

Table 2: Plastids transitions in to greening and non-greening types and genes of plastids that effects the growth and development of plant

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Color	Conversion	Species	Organ/ tissue/ cell	References
Greening	Proplastid to Chloroplast	Arabidopsis thaliana	Shoot apical meristem	Yadav et al., 2019
	Etioplast to Chloroplast Arabidopsis thaliana Nicotiana Leaf		<i>licotiana</i> Leaf	Pipitone et al., 2021
		tabacum		Armarego-Marriottetal.,2019
	Leucoplast to Chloroplast	Solanum tuberosum	Tuber	Tanios et al., 2018
Non-	Proplastid to Etioplast	Arabidopsis	thaliana Leaf Hypocotyl	Bykowski et al., 2020 Kakuszi
Greening		Phaseolus vulgaris		et al., 2017
-	Proplastid to Amyloplast	Musa acuminata	Fruit	Solis-Badillo et al., 2020
	Proplastid to Elaioplast	Arabidopsis thaliana	Citrus Pollen Outer peel of the	e Kobayashi and Masuda, 2016
		sinensis	fruit	Zhu et al., 2018
	Proplastid to Proteinoplast	Vigna radiata	Leaf	Dashek and Miglani,2017
	Proplastid to Chromoplast	Citrullus lanatus	Daucus Fruit Callus	Fang et al., 2020
		carota		Oleszkiewicz et al., 2018
	Leucoplast to Chromoplast	Oryza sativa	Transgenic	Bai et al., 2016
	Chloroplast to Chromoplast		Solanum Fruit	Jeong et al., 2020 Wang et al.,
	- · ·	2020		
De-greening	g Chloroplast to Gerontoplast	t Jatropha curcas	Seed inner integument	Shah et al., 2016

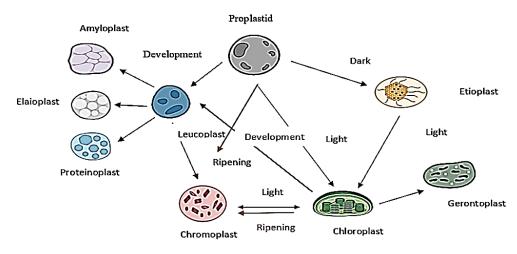


Fig. 2: shows the interconnections between different types of plastids. The classification of plastids features and interconversion routes was based on the color of arrow.

#### **Etioplasts**

Proper etioplasts are other intermediate types of plastids which are majorly present in the dark grown seedlings. Found in seedings which develop under the soil (Wietrzynski & Engel, 2023). They are the temporary stage of the development for chloroplasts and are known as the status of, the state of frugality because during this phase formation of the photosynthetic chemicals and structures which are not useful in the absence of light is stopped (Novoveská et al., 2023). In etioplasts in ordered single paracrystalline prolamellar body and tubular prothylakoids are developed and between them large amount of small plastoglobules with high concentrations of carotenoids and mainly lutein and violaxanthin which facilitate the transition into chloroplasts (Schramma et al., 2023).

#### Leucoplasts and Derivatives

Leucoplast are characterized by their structures that are white in colors (Sierra et al., 2023). Mainly we can encounter them in non chlorophyllian tissues which serve for storage purposes. But development of microscope and an addition of many detection methods enabled the classification of leucoplast in detail. Among the general class of white plastids, there are three subcategories of leucoplasts, which are amyloplasts, proteinoplasts, and elaioplasts with the exception of undeveloped proplastids. (Abbattista et al., 2024).

### Amyloplast

Amyloplasts can be described by the presence of stabilized starch grains, where high density starch is stored (de Barros Dantas et al., 2023). Lipids found to associate with amyloplast membranes during their development are free fatty acids, lysophospholipids, lysophosphatidyl choline, and lysophosphatidylethanolamine, which also become part of the starch granules. Amyloplasts are found in sink tissues such as seeds, fruits, tubers and roots but they may also be found at low frequency in other parts such as the leaves stems and roots for temporal storage (Kumar et al., 2023). However, it is guite surprising that the stability of the amyloplasts in certain circumstances while in Arabidopsis leaves it is observed that the accumulation and degradation of starch are rapid and rhythmic, depending on the photosynthetic activity or its absence. Starch granules are also observed within various types of plastids including chloroplasts. Apart from their storage role, the amyloplast from Arabidopsis roots was also play a role in gravitropism signal transduction (Kirkby et al., 2023).

### Proteinoplasts

Sometimes, protein bodies are located in the plastid

structures mainly in the cytosolic region are called proteinoplasts (Sierra et al., 2023). In general, proteinoplasts are preserved in many various types of cells and at more than one evolutionary stage of plastids. Hypothesized for its location and what it contains, proteinoplasts are believed to have a part to play in protein storage. Moreover, higher accumulation of proteinoplasts in tobacco root exhibited strong oxidase activity which may have specific role in this (Silva et al., 2023).

#### Elaioplast

Elaioplasts are recognized with ultrastructure's numerous hydrophobic components such as lipids and terpenoids. They are involved in biosynthesis of lipids, and storage, but they play a variety of roles in different tissues (Ali & Szabó, 2023). In citrus fruits, elaioplasts are transported to secretory cavities and may have major effects on flavor quality. The most important findings of the work are the following: the pollen, especially exine formation, was shown to be highly associated with elaioplasts.

#### Chromoplasts

Chromoplasts have characteristics as they accumulate large amounts of carotenoids and their different colors are determined by specific types of carotenoids (Arzac et al., 2022). In Plastoglobules which form globular, round, coiled shaped carotenoid crystals at the mature stage are produced and stored in hydrophobic structures during chromoplast development. The function of both lipid biosynthesis, storage and cleavage plastoglobules are present that are lipoprotein particles attached to thylakoids through a half-lipid bilayer (Arzac et al., 2022). These colored plastids developed plastoglobules that are used to attract pollinators and seed disseminators in reproductive tissues, storage of carotenoids and hydrophobic metabolites (Zhang, 2021).

#### Gerontoplast

Gerontoplasts are plastids having been modulated from chloroplasts and are specialized in recycling of the plastid they are mostly observed in the senescing tissues or under stress. Since entire nitrogen of a leaf can reach up to 80% of chloroplasts, their degradation is crucial for the plant's life since they cease to function and recycle their nutrients (MacDonald et al., 2023). And the degradation of chloroplast proteins has been described for three different processes, autophagy, during the initiation of the senescence process, there are dynamic alterations of plastids concerning their ultrastructure. As for gerontoplast, the characteristics of gerontoplasts at the early stage of senescence are still hard to define however. First gerontoplasts do not contain any starch granules likely due to the fact that gerontoplasts cannot do photosynthesis which restocks the starch every day. Second, they have damaged thylakoid structures and their chlorophyll have also been damaged (Tariq et al., 2023). Third, the size of their plastoglobules is larger and their number is higher, most likely because of the concentration of substances that are soluble in lipids as a result of degradation of lipid structures and hydrophobic components (Barros et al., 2023). Relationship among different type of plastids mention in Fig. 2.

# Specialized Types of Plastids (Desiccoplasts, Phenyloplasts, and Xyloplasts)

Desiccoplasts are specified plastids of the C3plants for the interconversion between chloroplasts and proplastids in the desiccation tolerant plants. Phenyloplasts are phenol enriched colorful plastids revealed as a different type of plastids to be compared to chromoplasts due to the differences in their storage substances and the homeostatic functions related to phenols(Wu, 2024). Xyloplasts are particularly found in tissues of secondary vascular system and are exclusively involved in synthesis of precursors essential in monolignol generation from proplastids or most probably amyloplasts (Altamura et al., 2024).

# Plastid Transitions that change of Chloroplast into Greening colors

#### **From Proplastids**

Transitions of proplastids to chloroplasts mainly occur in the shoot apical meristem and during embryogenesis (Table 1). Observations using Arabidopsis have revealed that differentiation from the shoot apical meristem of the young leaf can occur simultaneously with leaf formation. Differentiation takes place in the upper layer and the central subtending cell layers, it is independent of light intensity but requires a 5-10 hrs light phase. Studying embryogenesis of the model plant Arabidopsis, cells containing chloroplasts were detected at the globular stage of plant embrvogenesis. which provides evidence of chloroplasts' differentiation from proplastids (Bhat et al., 2024). In such in vitro conditions, the dark grown calluses contain only proplastids and the light grown calluses contain short thylakoids and chloroplasts with immature membrane system (Serafini-Fracassini & Del Duca, 2024).

#### **From Etioplasts**

During emergence of etioplasts to its photomorphogenic state, protochlorophyllide which is

the chlorophyll precursor of prolamellar bodies gets transformed to chlorophyllide by the action of light dependent NADPH (Partap et al., 2023). Subsequent to this, there are enzymatic processes through which chlorophyllide transforms to chlorophyll (Muthukumar, 2023).I. It is widespread in plant leaf tissues and it can be rather easily found in the plant kingdom, such as the internal leaves of white heads of a Brassica oleracea inner leaves of Lactuca sativa and the cotyledons of a Cucumis sativus. The studies conducted on tobacco leaves revealed that the physical constituents of the etioplast prolamellar bodies changed rapidly as soon as they are exposed to light and there were contraction in regularity and size (Bhatla & Lal, 2023). Recent work revealed that chloroplast biogenesis from etioplast into two distinct phases. One of the Phase of disassembly of prolamellar body, gradual formation of the thylakoid membrane and initial increase of galactolipid and proteins that relate with photosynthesis and the Chloroplast and the other phase is the Proliferation Phase for the cell expansion in which linear increase of eukaryotic galactolipid prokarvotic and and photosynthesis related proteins and increased grana stacking (Xu et al., 2024).

#### From Leucoplast

While it is true that some types of leucoplasts are non-developmental or non-photosynthetic, recent research shows that leucoplasts can be differentiated Different tissues of into chloroplasts. cortical parenchyma of the potato tubers just underlying the periderm contain amyloplasts which on exposure to light sources change into chloroplasts through the accumulation of chlorophylls (Lopez et al., 2024). In addition, the Norway spruce needle leaf also demonstrated the plastid transitions in accordance with growth and changes with the seasons. Our result showed that in Norway spruce, both amyloplasts for nutrient storage and chloroplasts for photosynthesis are differentiated at seedling stage (Watanabe et al., 2018). From the seasonal aspect, amyloplasts appears mainly because of large amounts of stored starch in the autumn and winter while transforming into ordinary chloroplasts in the spring and summer. In Italian Arum italicum, greening occurs later fruitlet formation (Altamura et al., 2024). To date, there have been no reports of any other fruit species exhibiting pre-fruitlet greening. It is observed as the chloroplast develops and the four amyloplast types are replaced with chloroplast having the plastoglobules and thylakoid membrane grows (Zhou et al., 2023).

#### **From Chromoplasts**

Cyclic changes from chromoplast to chloroplast known as regreening is reported in citrus, pumpkin and

cucumber fruits (Yen et al., 2024). As the fruit ripens the cucumber thylakoids are dissolved and later re-formed since there is regreening that occurs (Altamura et al., 2024). The process of reconstitution of thylakoids starts with membrane bound bodies and the rest are through the processes of surface expansion and fragmentation (Yilmazer et al., 2023). This transition suggests that a number of types of membrane structures are linked with the plastid envelope during chloroplast redifferentiation. The chlorophyll content of the tissue was found approximately to be two folds higher as compared to the unirradiated tissue after the time span of four weeks (Lafuente et al., 2024). Additionally, the treatment with light induced also the change of the identity of the roots of the carrots and of their chromoplasts into lutein-containing chloroplasts from βcarotene ones (Keawmanee et al., 2023).

#### Change of Proplastids into Etioplasts for Nongreening colors

It was also reported that proplastids may grow into etioplasts structures whereas the plant etiolates when seeds are bedded underground without direct source of light, although with suitable environmental signals for the germination process (Sajib et al., 2023). This transition is used by most plants and is sensible in lightavoidance under the circumstances especially for seedlings. As demonstrated in the studies on the model plant Arabidopsis and soybean etioplast formation is dependent on etiolation time while efficient arrangement of tubular-lamellar etioplast impacts on the subsequent vegetative growth. The absence of negative regulators for photomorphogenesis prevented the differentiation of etioplast in darkness therefore supporting the fact that etioplasts form in darkness due to the absence of photomorphogenesis (Brodrick & Jékely, 2023).

#### Change of Proplastids into Leucoplasts for Nongreening colors

#### **To Amyloplasts**

The development of amyloplasts structures in majority of tissues are those that contain high levels of starch. Carbohydrates are mainly deposited in the form of starch in the root tissues of plants and include Arabidopsis, flax and pea (Pusenkova et al., 2023). In addition, tubers and stolons of potatoes as representatives of accumulating amyloplasts has significance. In case of fruits, starch mainly stored at the "maturation" stage, for instance, in banana and Italian arum. In vitro study identified that amyloplasts differentiate in both callus and endosperm tissues in the case of apples. For rice and wheat, amyloplasts exist in the endosperm and they are layered up in the course of development (Kaushal et al., 2023). In amyloplasts, the starch biosynthesis occurs in the matrix space and the starch grains found there in display diverse morphological characteristics depending on plant species. The diameter of the starch grains size in corn  $10\mu m$ , rice  $10-20\mu m$  and sorghum are  $15-25\mu m$ , while it is found to be less than 10micro meter in barley and wheat (Delmer et al., 2024).

#### **To Elaioplasts**

The elaioplasts mostly present in flowers ovaries, ovary epidermis and anther wall (Rahim et al., 2023). Elaioplasts found in secretory channels of the stem and leaf epidermis in *Centaurea cyanus*, roots, young leaves of *Vanilla planifolia*, hypocotyls of the *Althaea rosea*, seeds of canola and sunflower, mesocarp of the fruit in avocados and green pericarps of citrus fruits (Choi et al., 2021). The formation of elaioplasts has been described to occur through a multiplicity of processes that seem to differ from species to species. In studying the differentiation of elaioplast in the tapetal cells of *Arabidopsis thaliana*, it was found that the change from proplastid to elaioplast occurs in "stage 9" and contains spot like structure which are shaped similar to the plastoglobuli (Costa & Demarco, 2024).

#### **To Proteinoplast**

Proteinoplasts starting from the roots of tobacco. It is mainly found in the vacuolated root cap cells and are concentrated in the slenderical tubules of the plastids (Sierra et al., 2023). During cell division, proteins accumulate tubules enlarge in size and protein are of spheroidal structure. In addition, the presence of proteinoplasts was also detected in localized tissues of the *Helleborus corsicus* leaves and Zea maize seeds. Moreover, a proteinoplast that are granular matrix harboring a great deal of protein in it was found in the leaves of mung bean plant (Filin & Platonova, 2024).

#### Change of Chloroplast into Chromoplasts for Nongreening colors

#### **From Proplastid**

The change from proplastids to chromoplasts is occurring through fruit ripening, for example, in Citrullus lanatus, Carica papaya, carrot callus (Altamura et al., 2024). Initially, the cells of ripening papaya contain undifferentiated proplastids only, while no chloropast and no amylopast are present; chromopast are directly formed in mature tissues of different natures. differentiation and Chromoplast carotenoids in fruit maturity watermelon increase with with plastoglobuli more in yellow and orange chromoplasts as compared to white (Hermanns et al., 2020). It could be seen that red chromoplasts in watermelon are of elongated structures with a higher plastoglobulus content (Gong et al., 2024). For example, in carrot callus, there is a transition from containing proplastids during differentiation, pale yellow callus contains mainly proplastids while dark orange callus contains many chromoplast which contains high carotenoids. Likewise, in Arabidopsis callus, over accumulation phytoene synthase leads to increase the level of carotenoids that in turn induces chromoplast differentiation.

#### **From Leucoplasts**

The change from proplastid to chromoplastic development takes place during development of the fruits, flowers and roots in Daucus carota and the orange cauliflower mutants Brassica oleracea var. botrytis (Hao et al., 2020). In fresh mature orange carrots roots, many chromoplasts carry crystalline carotene while, relatively fewer chromoplasts without the definite crystalline structures are seen in white immature carrots which have mostly amyloplasts with starch grains (de Souza Moretti et al., 2023). Orange cauliflower mutants contain β-carotene chromoplasts that are not present in leucoplasts of wild typical white tissues (Hermanns et al., 2020). Chromoplast transitions are found in the endosperm of rice and corn endothelial cells which is commonly developed of amyloplasts (Ďúranová et al., 2023). Wild-type rice endosperm does not contain any carotenoids, however, when several carotenogenic genes are introduced into the endosperm including genes for 1-deoxy-D-xylulose, 5-phosphate synthase, PSY and bacterial phytoene desaturase, chromoplasts are produced (Quian-Ulloa & Stange, 2021).

#### **From Chloroplasts**

Chromoplasts play role for the synthesis and accumulation of carotenoids and their location is most frequent in the petals and fruits since these organs are considered reproductive ones however chromoplasts may be present in the leaves and roots as well (Gong et al., 2024). Chromoplast formation from chloroplast occurs consideration of the degradation of thylakoids and chlorophyll, which marks the initial steps towards chromoplast formation (Aronsson & Solymosi, 2024). This is succeeded through biosynthesis, expansions of plastoglobuli size and also aggregation of the carotenins. the Examples illustrating mutually irreversible transformation from chloroplast to chromoplast done on Solanum lycopersicum red pepper Italian arum and Lilium longiflorum (Choi et al., 2021). Notably, in Arabidopsis single gene overexpression, the AtPSY lines and the phytoene synthase of Pantoea ananatis by viral vector in tobacco were able to differentiate the chromoplast from the leaf tissues (Morelli et al., 2023). Referring to the recent report on changes in membrane of tomato chloroplasts and found on the inner side of membranes envelope and thylakoid membranes vanished through the

transformation from chloroplast to chromoplast while new structure like plastoglobules and the crystal remains and so on was formed through budding and e fusion of membrane vesicles (Bykowski et al., 2020) (Table 2).

#### **Changes of Chloroplasts for De-Greening Colors**

#### **To Leucoplasts**

Arabidopsis flower changes is one of the example for de-greening to leucoplast (Choi et al., 2021). The young petals that have opened and which are still green bear chloroplasts in first but as the petals become larger, they have no chlorophyll and that are reconstructed into white bodies (Li et al., 2022). Plastids degenerate while chlorophyll is utilized and, in the meantime, carotenoids are not produced (Ling et al., 2021).

#### **To Gerontoplasts**

Gerontoplasts arises in the photosynthetic and nonphotosynthetic tissues of the plant form through aging process (Choi et al., 2021). In general, with the decline in the functional ability of the chloroplast, the outer shell is seen to be preserved while plastoglobuli along with lipophilic substances are formed and there are numerous structural changes in the thylakoid membrane (Garab et al., 2022). When gerontoplasts were observed in Arabidopsis it was revealed that these organelles were devoid of a sharply defined outer membrane, thylakoid membranes of chloroplast were also edematous with large and conspicuous plastoglobuli and grana and these features were found to gradually accumulate as the organelle aged (Ďúranová et al., 2023). One of the studies focused on the structural features of gerontoplasts during seed maturation of Jatropha curcas showed inner membrane system like thylakoid membrane, and outer envelope membrane of plastids that disassembled of substrate and the plastoglobuli.

#### **Chloroplast Growth**

Chloroplast development is regulated by light, detected by photoreceptors Such as UV-B/UVR8, UV-A/blue cryptochromes, phototropins and red/far-red phytochromes (Yadav et al., 2020). Light signals modulate chloroplast biogenesis with respect to E3 ligase mediated protein degradation. Regulators are the COP1-SPA1 complex, whose interactions are suppressed by activated UVR8 and CRY1 compacting the destruction of proteins such as HY5 that are vital for light reactions (Sutton, 2022). GLK factors are the first major activators of chloroplast differentiation, which, when protected from ubiquitination, remain stable (Cackett et al., 2022). Others which may play a role include the GATA factors. Fluorescence control of gene

expression increases chloroplast development process such as tetrapyrrole formation and PANG (Wang et al., 2022). Though OsGLK1 overexpression promote proplastid to chloroplasts transition, rice and other factors such as other GLKs regulation of light induced chloroplast development (Choi et al., 2021).

#### **Chromoplast Growth**

Chromoplast transition in fruit ripening is a multiregulatory process. In tomato, activation of carotenoid biosynthesis enzyme genes is done by the MADS-box transcription factor, RIN in collaboration with TAGL1 and AGAMOUS-like proteins (Li et al., 2023). There are some other factors which are involved such as, NAC factor non-ripening and bZIP factor HY5, which also regulates the transcription of PSY and phytoene desaturase. In Arabidopsis HY5 interacts with bHLH factors to facilitate proteins required for chloroplasts stability (Bulgakov & Koren, 2022). MrIG/FMD and stay green 1(sISGR1) repressor analyzed in tomato restrict chromoplast transformation through lowering the SIPSY1 level. Reducing the level of SISGR1 increases SIPSY1, thus accelerating the transformation to chromoplasts (Feng et al., 2023). It is revealed that MADS-box protein SICMB1 plays an important function in chromoplast differentiation as it involves the regulation of the expression of key enzymes and ethylene biosynthesis (Li et al., 2023). Many factors such as environmental and developmental are involved chromoplast formation through carotenoid in biosynthesis induction such as ripening factor.

#### Conclusion

By combining new developments in molecular biology, this review article offers the study of plastids and thorough comprehension of the various roles and activities of plastids that go beyond their conventional categories. This article dives into the lesser-studied plastids like proteinoplasts, etioplasts and gerontoplasts highlighting their emerging roles in plant development process, stress responses and metabolic regulation. In contrast to previous reviews that have primarily focused on specific plastid types such as chloroplasts and chromoplasts. Through highlighting the versatility and adaptability of plastids, the study offers fresh perspectives on their role in cellular communication, nutritional recycling, and environmental adjustment. The plastid genome encodes essential genes for basic plastid functions, while the nuclear genome provides additional genes necessary for the specialized roles of different plastid types. Understanding these genes and their interactions is crucial for studying plastid biogenesis, differentiation, and function, providing insights into plant physiology and development. The paper also explores how these discoveries may be used biotechnologically to improve crop resilience and nutrient efficiency, forging a link between fundamental plant biology and innovative agricultural practices. This review is unique in that it takes a thorough and integrated approach, providing a more comprehensive understanding of plastid biology and its implications for plant science and biotechnology. Lipid containing plastids called elaioplasts are present in various parts of the plants including flowers, fruits and seeds, as well as in young tissues. They are different kinds of granules in the course of organisms' formation and their differentiation pathways are species-unique. Elaioplast development in Arabidopsis thaliana involves the development of proplastid to different elaioplasts with plastoglobuli like structure. Further studies should focus on clarifying the molecular mechanisms that control the differentiation process of elaioplasts and the net of interactions regulating this process. Knowledge of these processes can give idea towards lipid metabolisms, storage system of cells and application in agriculture and bio technology.

#### Future perspective

Modern science and technology have positively enhanced plant characteristics by different methods that include controlling the spread of transgenes, disease resistance, and stress indicators, production of pharmaceuticals, and bio fuel. The emphasis has been shifted towards the engineering of traits through chloroplast genomes for the improvement of agronomic characteristics in the fruits and vegetables. Further studies will be required to understand how elaioplasts are formed in other species and how they are utilized in other developmental periods or throughout 'stage 9' in the Arabidopsis plant. Knowledge in lipid storage and utilization is useful and can improved oilseeds as well as better uses of plant lipids in agricultural biotechnology. It is important for research to be conducted that will focus on the process by which chloroplasts are converted to chromoplasts. Knowledge of molecular events and respective genes can enhance the quantity and quality of the crops as well as the nutritional values of the carotenoids and their distribution can be enhanced for commercial uses. Other research on the development of flowers in Arabidopsis can uncover ways on changing the coloration of flowers and the overall appearance to improve their ornamental value. Investigations on gerontoplasts might be useful for understanding the aging process of plants and the process of nutrient recycling, which in turn may push forward the development of technologies regarding increase of crop yield and stress tolerance. Comprehending chloroplast biogenesis and creating light expression of chloroplasts might optimize photosynthesis efficiency and stress discipline by genetically and bio syn- synthetically. Further, the understanding of chromoplasts during the process of fruit ripening and participation of such regulatory protein like RIN, HY5 and SISGR1 might enhance the nutritional balance and color of fruit. Heredity techniques like CRISPR/Cas9 could make improvement in the formation of the chromoplasts, thus improving the prospects of productivity, color and nutritive value of crops and therefore sustenance of agriculture and food security.

# REFERENCES

- Abbattista, R., Feinberg, N. G., Snodgrass, I. F., Newman, J. W., & Dandekar, A. M. (2024). Unveiling the "hidden quality" of the walnut pellicle: a precious source of bioactive lipids. Frontiers in Plant Science, 15, 1395543.
- Alghoul, E., Basbous, J., & Constantinou, A. (2023). Compartmentalization of the DNA damage response: Mechanisms and functions. DNA repair, *128*, 103524.
- Ali, O., & Szabó, A. (2023). Review of eukaryote cellular membrane lipid Composition, with special attention to the fatty acids. International Journal of Molecular Sciences, 24(21), 15693.
- Altamura, M. M., Piacentini, D., Della Rovere, F., Fattorini, L., Valletta, A., & Falasca, G. (2024). Transition dynamics in plastid interconversion in land plants. Plant Biosystems-An International Journal Dealing with all Aspects of Plant *Biology*, 1-31.
- Aronsson, H., & Solymosi, K. (2024). Diversification of Plastid Structure and Function in Land Plants. In *Plastids: Methods and Protocols* (pp. 63-88). Springer.
- Arzac, M. I., Fernández-Marín, B., & García-Plazaola, J. I. (2022). More than just lipid balls: quantitative analysis of plastoglobule attributes and their stress-related responses. Planta, 255(3), 62.
- Barros, J. A., Cavalcanti, J. H. F., Pimentel, K. G., Magen, S., Soroka, Y., Weiss, S., Medeiros, D. B., Nunes-Nesi, A., Fernie, A. R., & Avin-Wittenberg, T. (2023). The interplay between autophagy and chloroplast vesiculation pathways under dark-induced senescence. Plant, Cell & Environment, 46(12), 3721-3736.
- Bennett, G. M., Kwak, Y., & Maynard, R. (2024). Endosymbioses have shaped the evolution of biological diversity and complexity time and time again. Genome Biology and Evolution, evae112.
- Bhat, N., Bhatt, A., & Suleiman, M. (2024). *Physiology of Growth and Development in Horticultural Plants*. CRC Press.
- Bhatla, S. C., & Lal, M. A. (2023). Light perception and transduction. In *Plant Physiology, Development and Metabolism* (pp. 363-390). Springer.
- Brodrick, E., & Jékely, G. (2023). Photobehaviours guided by simple photoreceptor systems. Animal Cognition, 26(6), 1817-1835.
- Bulgakov, V. P., & Koren, O. G. (2022). Basic protein modules combining abscisic acid and light signaling in Arabidopsis. Frontiers in Plant Science, *12*, 808960.
- Bykowski, M., Mazur, R., Buszewicz, D., Szach, J., Mostowska, A., & Kowalewska, Ł. (2020). Spatial nanomorphology of the prolamellar body in etiolated Arabidopsis thaliana plants with disturbed pigment and polyprenol composition. Frontiers in Cell and Developmental Biology, *8*, 586628.
- Cackett, L., Luginbuehl, L. H., Schreier, T. B., Lopez-Juez, E.,

& Hibberd, J. M. (2022). Chloroplast development in green plant tissues: the interplay between light, hormone, and transcriptional regulation. New Phytologist, 233(5), 2000-2016.

- Chauhan, J., Singh, P., Choyal, P., Mishra, U. N., Saha, D., Kumar, R., Anuragi, H., Pandey, S., Bose, B., & Mehta, B. (2023). Plant photosynthesis under abiotic stresses: Damages, adaptive, and signaling mechanisms. Plant Stress, 100296.
- Chaux, F., Jarrige, D., Rodrigues-Azevedo, M., Bujaldon, S., Caspari, O. D., Ozawa, S. i., Drapier, D., Vallon, O., Choquet, Y., & de Vitry, C. (2023). Chloroplast ATP synthase biogenesis requires peripheral stalk subunits AtpF and ATPG and stabilization of atpE mRNA by OPR protein MDE1. The Plant Journal, *116*(6), 1582-1599.
- Choi, H., Yi, T., & Ha, S.-H. (2021). Diversity of plastid types and their interconversions. Frontiers in Plant Science, *12*, 692024.
- Choi, J. W., Graf, L., Peters, A. F., Cock, J. M., Nishitsuji, K., Arimoto, A., Shoguchi, E., Nagasato, C., Choi, C. G., & Yoon, H. S. (2020). Organelle inheritance and genome architecture variation in isogamous brown algae. Scientific Reports, 10(1), 2048.
- Chung, K. P., Gonzalez-Duran, E., Ruf, S., Endries, P., & Bock, R. (2023). Control of plastid inheritance by environmental and genetic factors. Nature plants, *9*(1), 68-80.
- Costa, E. R., & Demarco, D. (2024). Development and Holocrine Secretion of Resin Ducts in Kielmeyera appariciana (Calophyllaceae). Plants, *13*(13), 1757.
- de Barros Dantas, L. L., Eldridge, B. M., Dorling, J., Dekeya, R., Lynch, D. A., & Dodd, A. N. (2023). Circadian regulation of metabolism across photosynthetic organisms. The Plant Journal, *116*(3), 650-668.
- de Souza Moretti, M. M., Costa, M. S., Bai, Y., Gilbert, R. G., & de Souza Rocha, T. (2023). Structure of starch, focusing on those from underground plant organs. In *Starchy Crops Morphology, Extraction, Properties and Applications* (pp. 217-244). Elsevier.
- Delmer, D., Dixon, R. A., Keegstra, K., & Mohnen, D. (2024). The plant cell wall—dynamic, strong, and adaptable—is a natural shapeshifter. The Plant Cell, *36*(5), 1257-1311.
- Ďúranová, H., Šimora, V., Ďurišová, Ľ., Olexiková, L., Kovár, M., & Požgajová, M. (2023). Modifications in ultrastructural characteristics and redox status of plants under environmental stress: A review. Plants, 12(8), 1666.
- Feng, Y., Kou, X., Yuan, S., Wu, C., Zhao, X., Xue, Z., Li, Q., Huang, Z., & Sun, Y. (2023). CRISPR/Cas9-mediated SNAC9 mutants reveal the positive regulation of tomato ripening by SNAC9 and the mechanism of carotenoid metabolism regulation. Horticulture Research, 10(4), uhad019.
- Filin, V. R., & Platonova, A. G. (2024). Is there a tapetum in the hornwort capsule? Evidence from the sporogenesis of Phaeoceros. Botanical Journal of the Linnean Society, boae052.
- Fünfgeld, M. M., Wang, W., Ishihara, H., Arrivault, S., Feil, R., Smith, A. M., Stitt, M., Lunn, J. E., & Niittylä, T. (2022). Sucrose synthases are not involved in starch synthesis in Arabidopsis leaves. Nature Plants, 8(5), 574-582.
- Garab, G., Yaguzhinsky, L. S., Dlouhý, O., Nesterov, S. V., Špunda, V., & Gasanoff, E. S. (2022). Structural and

functional roles of non-bilayer lipid phases of chloroplast thylakoid membranes and mitochondrial inner membranes. Progress in Lipid Research, *86*, 101163.

- Gong, J., Li, Y., Shen, X., Xu, Y., Hu, X., Shen, D., Chen, C., & Sun, X. (2024). Diversity in plastids contributes to variation in fruit color. Scientia Horticulturae, 337, 113471.
- Gruber, A., & Medlin, L. K. (2023). Complex Plastids and the Evolution of the Marine Phytoplankton. Journal of Marine Science and Engineering, *11*(10), 1903.
- Gupta, P., Rodriguez-Franco, M., Bodanapu, R., Sreelakshmi, Y., & Sharma, R. (2022). Phytoene synthase 2 in tomato fruits remains functional and contributes to abscisic acid formation. Plant Science, 316(1), 111177.
- Hao, N., Han, D., Huang, K., Du, Y., Yang, J., Zhang, J., Wen, C., & Wu, T. (2020). Genome-based breeding approaches in major vegetable crops. Theoretical and Applied Genetics, *133*, 1739-1752.
- Hermanns, A. S., Zhou, X., Xu, Q., Tadmor, Y., & Li, L. (2020). Carotenoid pigment accumulation in horticultural plants. Horticultural Plant Journal, 6(6), 343-360.
- Ji, Y., Yue, L., Cao, X., Chen, F., Li, J., Zhang, J., Wang, C., Wang, Z., & Xing, B. (2023). Carbon dots promoted soybean photosynthesis and amino acid biosynthesis under drought stress: Reactive oxygen species scavenging and nitrogen metabolism. Science of the Total Environment, 856, 159125.
- Kaushal, M., Sharma, R., Vaidya, D., Gupta, A., Saini, H. K., Anand, A., Thakur, C., Verma, A., Thakur, M., & Priyanka, a. (2023). Maize: an underexploited golden cereal crop. Cereal Research Communications, *51*(1), 3-14.
- Keawmanee, N., Ma, G., Zhang, L., & Kato, M. (2023). Regulation of Chlorophyll and Carotenoid Metabolism in Citrus Fruit During Maturation and Regreening. Reviews in Agricultural Science, *11*, 203-216.
- Kirkby, E. A., Nikolic, M., White, P. J., & Xu, G. (2023). Mineral nutrition, yield, and source–sink relationships. In *Marschner's mineral nutrition of plants* (pp. 131-200). Elsevier.
- Kumar, A., P, N., Kumar, M., Jose, A., Tomer, V., Oz, E., Proestos, C., Zeng, M., Elobeid, T., & K, S. (2023). Major phytochemicals: recent advances in health benefits and extraction method. Molecules, 28(2), 887.
- Kuntz, M., Dimnet, L., Pullara, S., Moyet, L., & Rolland, N. (2024). The Main Functions of Plastids. Plastids: Methods and Protocols, 89-106.
- Lafuente, M. T., Sampedro, R., & Romero, P. (2024). Hormones metabolism as affected by LED blue light in citrus fruit. Plant Physiology and Biochemistry, *215*, 108970.
- Lazzarin, M. (2023). The role of far-red light in plant photosynthesis and photoprotection under artificial solar irradiance Wageningen University and Research].
- Lhee, D., Bhattacharya, D., & Yoon, H. S. (2024). The Evolutionary Origin of Primary Plastids. In *Endosymbiotic* Organelle Acquisition: Solutions to the Problem of Protein Localization and Membrane Passage (pp. 3-38). Springer.
- Li, M.-H., Liu, K.-W., Li, Z., Lu, H.-C., Ye, Q.-L., Zhang, D., Wang, J.-Y., Li, Y.-F., Zhong, Z.-M., & Liu, X. (2022). Genomes of leafy and leafless Platanthera orchids illuminate the evolution of mycoheterotrophy. Nature plants, 8(4), 373-388.
- Li, N., Wong, W. S., Feng, L., Wang, C., Wong, K. S., Zhang, N., Yang, W., Jiang, Y., Jiang, L., & He, J.-X. (2023). The

thylakoid membrane protein NTA1 is an assembly factor of the cytochrome b6f complex essential for chloroplast development in Arabidopsis. Plant Communications, 4(1), 100509.

- Ling, Q., Sadali, N. M., Soufi, Z., Zhou, Y., Huang, B., Zeng, Y., Rodriguez-Concepcion, M., & Jarvis, R. P. (2021). The chloroplast-associated protein degradation pathway controls chromoplast development and fruit ripening in tomato. Nature plants, 7(5), 655-666.
- Lopez, F., Barclay, G., & Badal, S. (2024). Plant anatomy and physiology. In *Pharmacognosy* (pp. 29-48). Elsevier.
- MacDonald, G., Lada, R. R., Caldwell, C., Udenigwe, C. C., & Maconald, M. T. (2023). Qualitative Assessment of Postharvest Stomata and Chloroplast Degradation in Contrasting Abscission Resistant Balsam Fir (Abies balsamea (L.) Mill.). American Journal of Plant Sciences, 14(9), 1009-1028.
- Morelli, L., Torres-Montilla, S., Glauser, G., Shanmugabalaji, V., Kessler, F., & Rodriguez-Concepcion, M. (2023). Novel insights into the contribution of plastoglobules and reactive oxygen species to chromoplast differentiation. New Phytologist, 237(5), 1696-1710.
- Muthukumar, S. S. (2023). Investigation of the redox signaling involved in the chloroplast biogenesis Université Grenoble Alpes [2020-....].
- Novoveská, L., Nielsen, S. L., Eroldoğan, O. T., Haznedaroglu, B. Z., Rinkevich, B., Fazi, S., Robbens, J., Vasquez, M., & Einarsson, H. (2023). Overview and challenges of large-scale cultivation of photosynthetic microalgae and cyanobacteria. Marine drugs, 21(8), 445.
- Partap, M., Sharma, D., Deekshith, H., Thakur, M., Verma, V., & Bhargava, B. (2023). Microgreen: A tiny plant with superfood potential. Journal of Functional Foods, 107, 105697.
- Pusenkova, L., Lastochkina, O., & Ercişli, S. (2023). The potential of hydroponic seed minituber enrichment with the endophyte Bacillus subtilis for improving the yield components and quality of potato (Solanum tuberosum L.). Agriculture, *13*(8), 1626.
- Quian-Ulloa, R., & Stange, C. (2021). Carotenoid biosynthesis and plastid development in plants: the role of light. International Journal of Molecular Sciences, 22(3), 1184.
- Rahim, M. A., Ayub, H., Sehrish, A., Ambreen, S., Khan, F. A., Itrat, N., Nazir, A., Shoukat, A., Shoukat, A., & Ejaz, A. (2023). Essential components from plant source oils: A review on extraction, detection, identification, and quantification. Molecules, *28*(19), 6881.
- Roca, M., Chen, K., & Pérez-Gálvez, A. (2024). Chlorophylls. In Handbook on natural pigments in food and beverages (pp. 193-226). Elsevier.
- Sajib, S. A., Kandel, M., Prity, S. A., Oukacine, C., Gakière, B., & Merendino, L. (2023). Role of plastids and mitochondria in the early development of seedlings in dark growth conditions. Frontiers in Plant Science, 14, 1272822.
- Sakamoto, W., & Takami, T. (2024). Plastid inheritance revisited: emerging role of organelle DNA degradation in angiosperms. *Plant and Cell Physiology*, 65(4), 484-492.
- Schramma, N., Perugachi Israëls, C., & Jalaal, M. (2023). Chloroplasts in plant cells show active glassy behavior under low-light conditions. Proceedings of the National Academy of Sciences, 120(3), e2216497120.
- Serafini-Fracassini, D., & Del Duca, S. (2024). Programmed Cell Death Reversal: Polyamines, Effectors of the U-Turn

from the Program of Death in Helianthus tuberosus L. International Journal of Molecular Sciences, *25*(10), 5386.

- Seung, D. (2020). Amylose in starch: towards an understanding of biosynthesis, structure and function. New Phytologist, 228(5), 1490-1504.
- Sierra, J., Escobar-Tovar, L., & Leon, P. (2023). Plastids: diving into their diversity, their functions, and their role in plant development. Journal of Experimental Botany, *74*(8), 2508-2526.
- Silva, O. F., Guimarães, A. L., Borges, R. M., Andrade, C. T., & Calado, V. (2023). Ultrastructural study of Manihot esculenta amyloplast: intragranular channels and membrane lipid profiling. Brazilian Journal of Botany, 46(1), 139-151.
- Skrzypkowski, W., & Kiełkowska, A. (2024). Current Status of Haploidization in Cool-Season Grain Legume Crop Species. Agriculture, 14(7), 1031.
- Srivastava, P., Sahgal, M., & Paul, S. (2024). Nitrogen-fixing Rhizobium-legume symbiosis in agroecosystems. In *Plant Endophytes and Secondary Metabolites* (pp. 35-54). Elsevier.
- Sutton, P.(2022). Advancing understanding of LED light impacts on plant phytonutrient content for application into hydroponically grown leafy greens. Lancaster University (United Kingdom).
- Tariq, A., Zeng, F., Graciano, C., Ullah, A., Sadia, S., Ahmed, Z., Murtaza, G., Ismoilov, K., & Zhang, Z. (2023).
  Regulation of metabolites by nutrients in plants. Plant lonomics: Sensing, Signaling, and Regulation, 1-18.
- Taylor, R. E., West, C. E., & Foyer, C. H. (2023). WHIRLY protein functions in plants. Food and Energy Security, *12*(2), e379.
- Tikhonov, A. N. (2014). The cytochrome b6f complex at the crossroad of photosynthetic electron transport pathways. *Plant Physiology and Biochemistry*, *81(1)*, 163-183.
- Völkner, C., Holzner, L. J., Bünger, K., Szulc, B., Lewis, C. M., Klingl, A., & Kunz, H. H. (2024). Evidence for partial functional overlap of KEA and MSL transport proteins in the chloroplast inner envelope of Arabidopsis thaliana. *FEBS letters*.
- Wang, F., Dischinger, K., Westrich, L. D., Meindl, I., Egidi, F., Trösch, R., Sommer, F., Johnson, X., Schroda, M., & Nickelsen, J. (2023). One-helix protein 2 is not required for the synthesis of photosystem II subunit D1 in Chlamydomonas. Plant Physiology, 191(3), 1612-1633.
- Wang, M., Zhu, X., Li, Y., & Xia, Z. (2020). Transcriptome analysis of a new maize albino mutant reveals that zetacarotene desaturase is involved in chloroplast development and retrograde signaling. Plant Physiology and Biochemistry, 156(1), 407-419.
- Wang, P., Ji, S., & Grimm, B. (2022). Post-translational regulation of metabolic checkpoints in plant tetrapyrrole biosynthesis. Journal of Experimental Botany, 73(14), 4624-4636.
- Watanabe, M., Netzer, F., Tohge, T., Orf, I., Brotman, Y., Dubbert, D., Fernie, A. R., Rennenberg, H., Hoefgen, R., & Herschbach, C. (2018). Metabolome and lipidome profiles of populus× canescens twig tissues during annual

growth show phospholipid-linked storage and mobilization of C, N, and S. Frontiers in Plant Science, *9*, 1292.

- Wietrzynski, W., & Engel, B. D. (2023). Supramolecular organization of chloroplast membranes. In *The Chlamydomonas Sourcebook* (pp. 763-785). Elsevier.
- Wu, A. (2024). A new model of chloroplast biogenesis from the perspective of the poikilochlorophyllous resurrection plant, Eragrostis nindensis ResearchSpace@ Auckland].
- Xu, H.-F., Yu, C., Bai, Y., Zuo, A.-W., Ye, Y.-T., Liu, Y.-R., Li, Z.-K., Dai, G.-Z., Chen, M., & Qiu, B.-S. (2024). Red-lightdependent chlorophyll synthesis kindles photosynthetic recovery of chlorotic dormant cyanobacteria using a darkoperative enzyme. Current Biology.
- Yadav, A., Singh, D., Lingwan, M., Yadukrishnan, P., Masakapalli, S. K., & Datta, S. (2020). Light signaling and UV-B-mediated plant growth regulation. Journal of Integrative Plant Biology, 62(9), 1270-1292.
- Yamamoto, H., Kojima-Ando, H., Ohki, K., & Fujita, Y. (2020). Formation of prolamellar-body-like ultrastructures in etiolated cyanobacterial cells overexpressing lightdependent protochlorophyllide oxidoreductase in Leptolyngbya boryana. The Journal of General and Applied Microbiology, 66(2), 129-139.
- Yang, P., Li, Y., He, C., Yan, J., Zhang, W., Li, X., Xiang, F., Zuo, Z., Li, X., & Zhu, Y. (2020). Phenotype and TMTbased quantitative proteomics analysis of Brassica napus reveals new insight into chlorophyll synthesis and chloroplast structure. Journal of Proteomics, 214(1), 103621.
- Yen, C.-C., Hsu, C.-M., Jiang, P.-L., & Jauh, G.-Y. (2024). Dynamic organelle changes and autophagic processes in lily pollen germination. Botanical Studies, 65(1), 5.
- Yilmazer, I., Vetrano, P., Eicke, S., Abt, M. R., Traverso, E., Morosinotto, T., Zeeman, S. C., Ramundo, S., & Sharma, M. (2023). A conserved ESCRT-II-like protein participates in the biogenesis and maintenance of thylakoid membranes. *bioRxiv*, 2023.2010. 2010.561251.
- Zayed, O., Hewedy, O. A., Abdelmoteleb, A., Ali, M., Youssef, M. S., Roumia, A. F., Seymour, D., & Yuan, Z.-C. (2023). Nitrogen journey in plants: From uptake to metabolism, stress response, and microbe interaction. Biomolecules, 13(10), 1443.
- Zhang, A., Tian, L., Zhu, T., Li, M., Sun, M., Fang, Y., Zhang, Y., & Lu, C. (2024). Uncovering the photosystem I assembly pathway in land plants. Nature plants, 10(4), 645-660.
- Zhang, Z. (2021). Supramolecular organisation, assembly, and regulation of cyanobacterial thylakoid membrane. The University of Liverpool (United Kingdom).
- Zhao, Z., Liu, Z., & Mao, X. (2020). Biotechnological advances in lycopene β-cyclases. Journal of Agricultural and Food Chemistry, *68*(43), 11895-11907.
- Zhou, Q., Karunarathne, P., Andersson-Li, L., Chen, C., Opgenoorth, L., Heer, K., Piotti, A., Vendramin, G. G., Nakvasina, E., & Lascoux, M. (2023). Recurrent hybridization and gene flow shaped Norway and Siberian spruce evolutionary history over multiple glacial cycles. Molecular Ecology, e17495.