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Illuminating colors: regulation of carotenoid biosynthesis and accumulation by light

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Light stimulates the biosynthesis of carotenoids and regulates the development of plastid structures to accommodate these photoprotective pigments. Work with Arabidopsis revealed molecular factors coordinating carotenoid biosynthesis and storage with photosynthetic development during deetiolation, when underground seedlings emerge to the light. Some of these factors also adjust carotenoid biosynthesis in response to plant proximity (*i.e.*, shade), a mechanism that was readapted in tomato to monitor fruit ripening progression. While light positively impacts carotenoid production and accumulation in most cases, total carotenoid levels decrease in roots of colored carrot cultivars when illuminated. The recent discovery that such cultivars might be photomorphogenic mutants provides an explanation for this striking phenotype.

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Introduction

As sessile organisms that rely on sunlight as the main source of energy, plants have developed sophisticated systems to sense and respond to light cues. Light regulates plant development right after germination. When seeds from angiosperm plants germinate in the dark, seedlings develop skotomorphogenetically (*i.e.*, with long hypocotyls and closed cotyledons harboring etioplasts with no chlorophylls and very little carotenoid contents). Upon illumination, however, a completely different developmental program unfolds: photomorphogenesis. The deetiolation process involves the inhibition of hypocotyl growth, the expansion of cotyledons, and the differentiation of etioplasts into chloroplasts with the concomitant production of high levels of chlorophylls and carotenoids. The main role of carotenoids in chloroplasts is to protect the photosynthetic apparatus against photooxidative damage caused by excessive illumination [1••,2]. Oxidative cleavage of carotenoids can produce retrograde signals such as β-cyclocitral to regulate the expression of nuclear genes in response to photooxidative stress, whereas their enzymatic cleavage generates hormones (abscisic acid and strigolactones) and other signaling molecules whose identity is still unknown [3]. Carotenoids also function as pigments, accumulating at massive levels in specialized plastids called chromoplasts [2]. Chromoplast carotenoids are hence responsible for the yellow color of corn, the orange color of carrots, and the red color of tomatoes. Humans cannot produce carotenoids but take them in the diet as an essential source of retinoids (including vitamin A) and other health-related biologically-active metabolites [2–4].

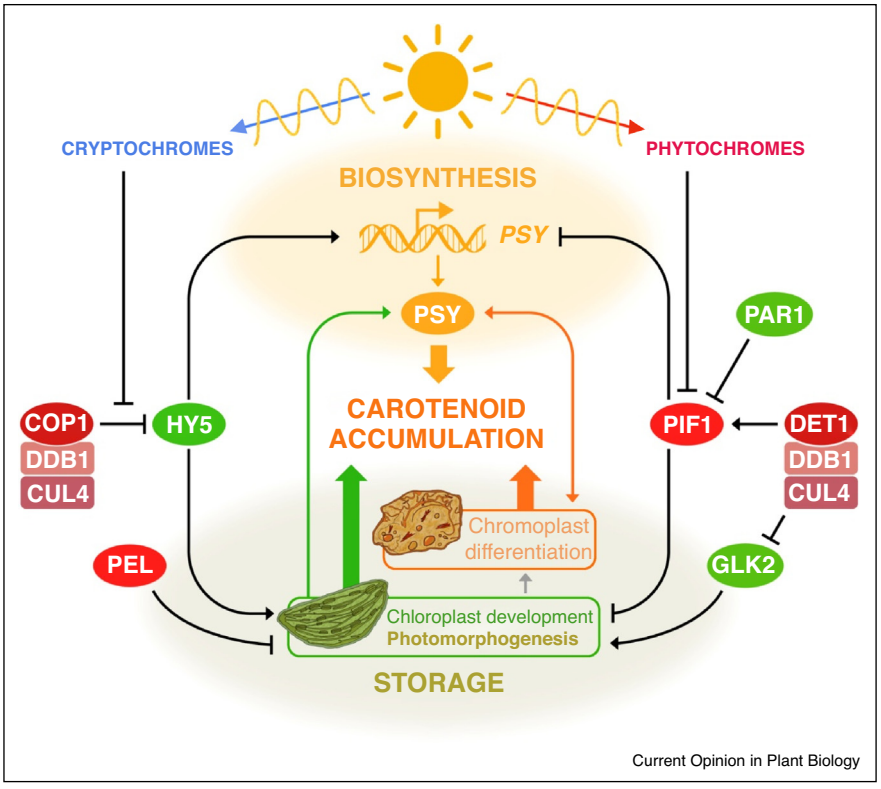
Despite the relevance of carotenoids for agriculture and health, we still have a limited knowledge on how plants regulate their synthesis and accumulation. Molecular mechanisms have been described to control (1) expression of genes involved in carotenoid biosynthesis and degradation, (2) activity of the corresponding enzymes, and (3) development of carotenoid storage structures in plastids. All three mechanisms are tightly coordinated by both developmental (internal) and environmental (external) signals, with light having a major role [2,4–8]. In this article we will focus on the molecular mechanisms by which light signals are transduced to regulate carotenoid biosynthesis at the level of phytoene synthase (PSY), the first and main rate-determining enzyme of the carotenoid pathway. We will also revise the impact of light signaling on carotenoid storage capacity through the regulation of plastid development and differentiation. In particular, we will cover three case studies involving different scenarios of light-regulated carotenoid accumulation: *Arabidopsis thaliana* deetiolating and shade-exposed seedlings, tomato (*Solanum lycopersicum*) ripening fruits, and carrot (*Daucus carota*) roots.

Case-study 1: Arabidopsis seedlings. Emerging to light

During deetiolation, the production of carotenoids is boosted at the biosynthetic gene expression and enzyme

activity levels [4,9]. At the same time, etioplasts differentiate into chloroplasts, which have a much higher capacity to accommodate the newly produced carotenoids. The molecular factors directly coordinating carotenoid biosynthesis and storage (*i.e.*, chloroplast differentiation) were discovered mainly using Arabidopsis deetiolation as a model system. Perception of light by photoreceptors such as cryptochromes (receptors of blue light) and phytochromes (receptors of red (R) and far-red (FR) light) is transduced by transcription factors to regulate photomorphogenesis (Figure 1). The expression of the only Arabidopsis gene encoding PSY is under the direct control of two of these transcription factors: PHYTOCHROME INTERACTING FACTOR 1 (PIF1) and LONG HYPOCOTYL 5 (HY5) [10•,11••]. PIF1 and other members of the so-called PIF quartet (formed by PIF1, PIF3, PIF4 and PIF5, collectively referred to as PIFq) belong to a bHLH subfamily of phytochrome-regulated transcription factors that typically accumulate in the dark and degrade in the light [12]. By contrast, the bZIP transcription factor HY5 is degraded in the dark but accumulates in the light [13]. PIFq and HY5 act antagonistically for a broad set of photomorphogenic responses. In the case of photosynthetic development, PIFq proteins are repressors and HY5 is an activator (Figure 1). High levels of PIFq and low levels of HY5 in etiolated seedlings block photosynthetic development (including carotenoid biosynthesis and chloroplast development). During deetiolation, light-mediated degradation of PIF1 (a direct repressor of *PSY* expression) and stabilization of HY5 (an

Figure 1



Schematic representation of light-related molecular pathways impacting carotenoid biosynthesis and storage in plants. Sunlight is perceived by photoreceptors such as cryptochromes (receptors of blue light) and phytochromes (receptors of R and FR light). Photoreceptors then transduce the light signal by regulating the stability of transcription factors such as PIF1 (a repressor of photomorphogenesis degraded in the light upon interaction with photoactivated phytochromes) and HY5 (an activator of photomorphogenesis degraded in the dark upon interaction with COP1). COP1 acts as a substrate receptor of the CUL4-DDB1 E3 ligase, which mediates the ubiquitination of substrates for degradation by the 26S proteasome (revised in Ref. [13]). Besides HY5, another COP1 client appears to be PAR1, a transcription cofactor that prevents PIF1 binding to the promoters of target genes, including *PSY* [16•,18]. The photomorphogenesis repressor DET1 can also bind to the CUL4-DDB1 complex and directly interact with Arabidopsis PIF1 to stabilize it [46,47] and with tomato GLK2 (a promoter of chloroplast development in the fruit) to target it to proteasome-mediated degradation [34]. Photomorphogenesis is additionally repressed by PEL [43••]. In carrot roots and tomato fruits, but not in Arabidopsis seedlings, chloroplasts can differentiate into chromoplasts. Development of chloroplasts and, to a higher level, chromoplasts increases deposition sink capacity for carotenoids and improves PSY activity. PSY activity is also regulated at the gene expression level. PIF1 proteins directly repress the expression of PSY-encoding genes in Arabidopsis and tomato fruit, whereas HY5 is a direct activator of the Arabidopsis *PSY* gene [10•,11••,31••]. Together, these positive (in green) and negative (in red) regulatory factors coordinate carotenoid biosynthesis and storage in a highly interconnected fashion.