Review

Synthesis and Function of Apocarotenoid Signals in Plants

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In plants, carotenoids are essential for photosynthesis and photoprotection. However, carotenoids are not the end products of the pathway; apocarotenoids are produced by carotenoid cleavage dioxygenases (CCDs) or non-enzymatic processes. Apocarotenoids are more soluble or volatile than carotenoids but they are not simply breakdown products, as there can be modifications post-cleavage and their functions include hormones, volatiles, and signals. Evidence is emerging for a class of apocarotenoids, here referred to as apocarotenoid signals (ACSs), that have regulatory roles throughout plant development beyond those ascribed to abscisic acid (ABA) and strigolactone (SL). In this context we review studies of carotenoid feedback regulation, chloroplast biogenesis, stress signaling, and leaf and root development providing evidence that apocarotenoids may fine-tune plant development and responses to environmental stimuli.

Trends

Apocarotenoids regulate plant development and may function as signals in response to stress.

Apocarotenoids are proposed to fine-tune carotenoid biosynthesis flux.

Apocarotenoid formation is largely dependent on the specificities of the CCD family of enzymes.

Apocarotenoid formation is regulated by developmental and environmental stimuli and subcellular compartmentalization.

Carotenoids and Apocarotenoids

Carotenoids are lipid-soluble isoprenoid compounds based on a C_{40} polyene backbone with varying degrees of double bond conjugation [1,2] (Figure 1). In nature, carotenoids are synthesized by all photosynthetic organisms (i.e., cyanobacteria, algae, higher plants) as well as some non-photosynthetic organisms such as fungi and bacteria [3,4]. Carotenoids are the basis for many pigments, scents in flowers, and aromas in fruits and aid in attracting pollinators and seed-dispersing organisms. Chloroplast-associated carotenoids also stabilize membranes and act as structural and accessory pigments in photosystems (PSs) and light-harvesting antennae, thereby protecting the photosynthetic apparatus from photooxidative damage [3]. In etiolated seedlings, carotenoids are required to form prolamellar bodies (PLBs), the lattices of tubular membranes that define etioplasts and accelerate photomorphogenesis on illumination [5,6]. Carotenoids are also precursors of the phytohormones ABA and SL (see reviews in [7,8]). They are also important to human health, being precursors of retinol (vitamin A) [9], acting as antioxidants [10], and being linked to reducing age-related macular degeneration and the risk of certain cancers [11,12].

Enzymatic and non-enzymatic oxidative cleavage of carotenoids produces biologically important carotenoid derivatives, apocarotenoids. CCD enzymes catalyze carotenoid cleavage at specific double bonds [13]. Non-enzymatic apocarotenoid formation can occur via singlet oxygen ($^1O_2$) attack, primarily on β-carotene [14]. Regardless of metabolic origin, apocarotenoids help fine-tune carotenogenesis and plant development and environmental responses, in part via changes in nuclear gene expression, and retrograde (plastid-to-nucleus) signaling [15]. Apocarotenoids have also been shown to inhibit mammalian cancer cell proliferation by altering gene expression [16]. Thus, the discovery and characterization of novel carotenoid derivatives *in planta* provide

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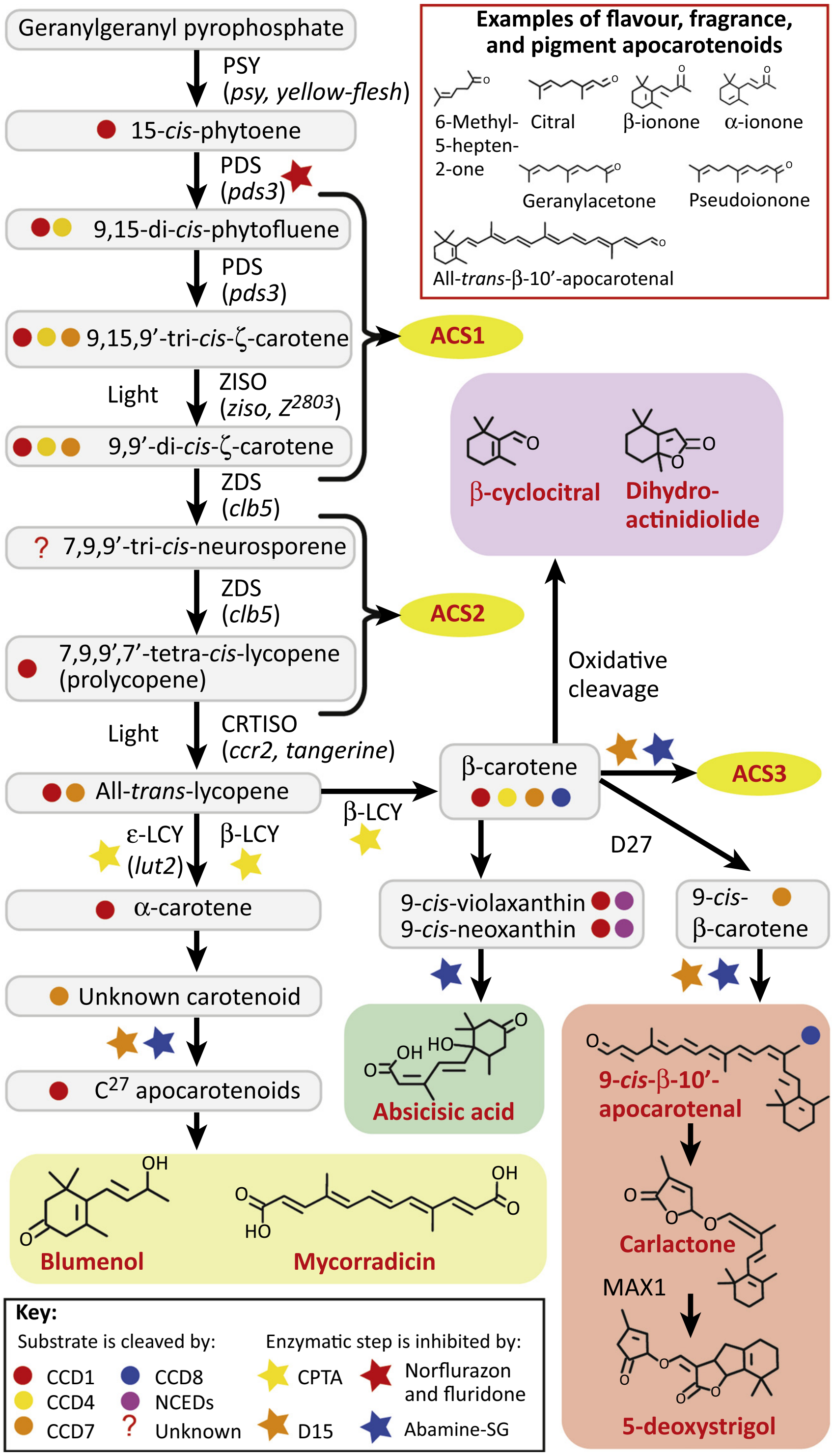

Figure 1. Apocarotenoid Biosynthesis. Many carotenoids are cleaved to form apocarotenoids through enzymatic reactions. Nine-*cis*-epoxy-dioxygenase (NCED) cleaves 9-*cis*-violaxanthin and 9-*cis*-neoxanthin to yield the precursor of abscisic acid (ABA). The carotenoid cleavage dioxygenase (CCD) enzymes cleave carotenoids to yield various apocarotenoids. CCD7 and CCD8, for example, contribute to strigolactone synthesis following β-carotene isomerization by D27.

(Figure legend continued on the bottom of the next page.)