

Photo-Oxidative Stress during Leaf, Flower and Fruit Development¹[OPEN]

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Chloroplasts are essential for plant growth and development through their roles in photosynthesis and signaling. Reactive oxygen species (ROS) and antioxidants play crucial roles in regulating developmental processes, from organ initiation to senescence, not only in leaves but also in some types of flowers and fruits. Flowers and fruits bearing chloroplasts during their early stages of development share some similarities with leaves but also important differences in terms of photosynthesis-derived ROS, the duration and extent of photooxidative stress, and redox signaling. Here, we discuss recent advances in our understanding of the common mechanisms underlying redox signaling in leaves, flowers, and fruits, focusing on key spatiotemporal processes that determine specific responses in each organ. Chloroplasts play a central role in cellular processes during organ development, with photooxidative stress a key effector of redox signaling during organ development in leaves as well as in some types of flowers and fruits.

The growth and development of organs are characterized by several well-defined and interconnected key stages. Organ initiation, marked by pluripotent meristematic cells that divide and differentiate to become a new organ, is followed by organ growth, which involves further cell proliferation through reiterative mitotic cycles and subsequent cell expansion. Maturity defines the stage when cells no longer expand and the organ reaches a fully competent state. Lastly, senescence is the final developmental stage of a plant organ, usually leading to programmed cell death (Beemster et al., 2005; Anastasiou and Lenhard, 2007; Thomas, 2013). Since different organs share this characteristic set of developmental events, it is possible that similar underlying regulatory mechanisms might be involved. However, although leaves and petals have common

evolutionary origins (Friedman et al., 2004), leaves, flowers, and fruits have completely different functions in plant development. Leaves transform light energy into chemical energy to provide photoassimilates, while petals enable pollination and, therefore, sexual reproduction and fruits, in turn, facilitate seed dispersal.

Several types of petals and fruits contain functional chloroplasts at early stages of development. However, the spatiotemporal dynamics of plastid differentiation differs between leaves, flowers, and fruits. In general, chloroplasts of mesophyll cells remain active during most of leaf ontogeny (until they become gerontoplasts in the last senescing stage), although loss of the cytochrome *b₆f* complex, electron flow, and proton conductivity may start earlier than chlorophyll degradation (Schöttler et al., 2017). By contrast, chloroplasts rapidly differentiate into chromoplasts in flower corollas, even before anthesis (Ščepánková and Hudák, 2004; Gan and Fischer, 2007; Arrom and Munné-Bosch, 2012) or during the ripening of the fruit exocarp (Lytovchenko et al., 2011; Lado et al., 2015). Chloroplast differentiation into gerontoplast typically occurs in senescing leaves (either yellow/orange or anthocyanin-rich red leaves), while chloroplast differentiation into chromoplast occurs in the flowers of some species (e.g. tepals from lilies [*Lilium* spp.] that turn from green to yellow or whitish) and several types of fruits (e.g. citrus fruits such as lemons [*Citrus limon*] and oranges [*Citrus sinensis*]). Indeed,

ADVANCES

- Chloroplast-related retrograde signaling is essential for organ development.
- Photooxidative stress is strongly dependent on environmental conditions, but also on the type of organ and its developmental stage.
- Redox signaling plays a key role in plastid differentiation in leaves, flowers, and fruits.
- Photooxidative stress may trigger redox signaling during organ development with important spatiotemporal differences between leaves, flowers, and fruits.

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flower and fruit development is incredibly diverse, with some of the color changes involved not always detected by our retinas. For instance, experiments with petunia (*Petunia hybrida*) flowers have shown that expanded pink corollas contain photosynthetically active chloroplasts with high chlorophyll content (compared with the very early green stages), thus suggesting that chloroplasts also can play specific roles in flower development in anthocyanin-rich reddish petals, at least in some species (Katz and Weiss, 1998).

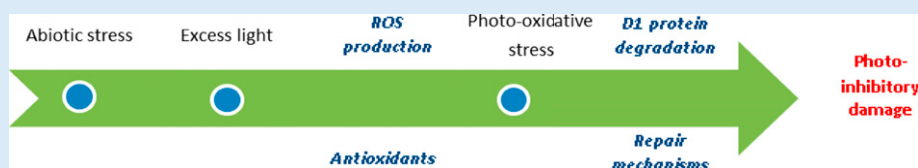
As aerobic organisms, plants cannot avoid ROS formation. In leaves, ROS production occurs mainly in chloroplasts, peroxisomes, mitochondria, and the apoplast due to the redox-related processes occurring in these organelles (Takahashi and Badger, 2011). Excessive levels of light in chloroplasts, caused by drought, salinity, extreme temperatures, high levels of light, or a combination of these factors, lead to photoinhibition and photooxidative stress, thus potentially causing photoinhibitory damage to the photosynthetic apparatus (Box 1). Although it is generally assumed that mitochondria, peroxisomes, and the apoplast are the main sources of ROS in flowers and fruits (Qin et al., 2009b; Rogers and Munné-Bosch, 2016), flower corollas and fruit exocarps in several species also accumulate excessive levels of light during the early developmental stages, generally until organ maturation is reached. Thus, photoinhibition and photooxidative stress also can occur in these organs (Arrom and Munné-Bosch, 2010; Hengari et al., 2014; Naschitz et al., 2015; Gang

et al., 2016). ROS are known to be toxic, but recent studies have indicated that ROS are involved in signaling during growth, development, and responses to biotic/abiotic stress (Bell et al., 2009; Xia et al., 2015). ROS signaling is tightly regulated, their production and elimination being controlled by antioxidants that determine the lifetime and specificity of the ROS signal (Foyer and Noctor, 2005a; Mittler et al., 2011). ROS with different natures generate distinct signals. For example, singlet oxygen ($^1\text{O}_2$) is a very reactive species that lasts only a few microseconds, while hydrogen peroxide (H_2O_2) is more stable, with a longer lifespan and a greater diffusion distance, which makes it a more likely molecule to trigger a transduction signal to the nucleus. Moreover, site formation and detoxification systems ultimately determine the specificity of the oxidative signaling processes (Foyer and Noctor, 2005b; Munné-Bosch et al., 2013; Mignolet-Spruyt et al., 2016). There are several questions regarding the role of ROS in plant organ development. For example, what types of ROS are produced in the chloroplasts of flowers and fruits compared with those in leaves? Can chloroplasts play a role in redox signaling during the growth and development of flowers and fruits? To what extent do chromoplasts contribute to cellular redox signaling during flower and fruit development?

Although the biology of ROS production and elimination in chloroplasts and its implications for redox signaling have been reviewed in the last 5 years (Munné-Bosch et al., 2013; Dietz et al., 2016), a comparative analysis of the role of photooxidative stress and chloroplast-derived redox

BOX 1. Basic Concepts Related to Photooxidative Stress in Plants

- **Antioxidant:** Enzyme or low molecular weight compound that prevents the oxidation of essential cellular components (e.g. lipids, proteins, nucleic acids).
- **Excess light:** amount of light not used for photosynthesis that may be dissipated to prevent damage in chloroplasts.
- **Photoinhibition:** inhibition of photosynthesis at the photosystem II level (reduction in photosystem II quantum yield).
- **Photoinhibitory damage:** injuries caused by excess light in chloroplasts; it can be reversible or not (depending on the severity and duration of excess light).
- **Photooxidative stress:** oxidative stress caused by excess light in chloroplasts.
- **Photooxidative damage:** photoinhibitory damage associated with oxidative stress.
- **Oxidative stress:** imbalance between reactive oxygen production and its elimination.
- **Reactive oxygen species (ROS):** unstable compound derived from molecular oxygen.
- **Redox signalling:** cell signalling based on reduction/oxidation processes.
- **ROS quenching:** Physical elimination of reactive oxygen species.
- **ROS scavenging:** Chemical elimination of reactive oxygen species.



signals in leaves, flowers, and fruits is still lacking. Here, we aim to go beyond our previous comparative analysis of ROS production and elimination in leaves and flowers (Rogers and Munné-Bosch, 2016) by providing a new conceptual framework for chloroplasts as central players in redox signaling in leaf, flower, and fruit development. This review will discuss recent advances in our understanding of photooxidative stress and redox signaling in leaves, flowers, and fruits, focusing on key spatiotemporal processes that determine specific responses in each organ. This might have important applications in agri-food biotechnology for the commercialization of leafy vegetables, flowers, and fruits.

CHLOROPLASTS IN LEAF, FLOWER, AND FRUIT DEVELOPMENT

Chloroplasts play a central role in cellular energy and redox processes. One of the most important events in the history of life was the origin of oxygenic photosynthesis. Life would not have been possible without the changes in atmospheric composition produced 2 billion years ago by ancient photosynthetic prokaryotes similar to cyanobacteria. The subsequent symbiosis of these photosynthetic organisms with eukaryotic cells gave rise to chloroplasts, powerhouse organelles that are now present in leaves and other photosynthetic tissues (Allen, 2015). In leaves, chloroplasts perform photosynthesis and are essential for C, N, and S reduction and assimilation (Kopriva and Rennenberg, 2004) as well as for the biosynthesis of amino acids, fatty acids, chlorophylls, and carotenoids, the latter essential for both the photosynthetic and antioxidant machinery (Joyard et al., 2009). Moreover, chloroplasts contribute to the production of phytohormones, such as abscisic acid, GA, auxins, salicylates, jasmonates, and melatonin, and essential antioxidants, such as vitamin E (Joyard et al., 2009). Chloroplasts also play a crucial role in redox processes and retrograde signaling, which are translated into metabolic changes through genetic regulation and control of the cellular redox state (Pfannschmidt, 2003; Asada, 2006; Dietz et al., 2016). However, during leaf senescence induced by aging and/or environmental stress, leaf chloroplasts change from a source to a sink due to a lower photosynthetic rate elicited by the disassembly of the photosynthetic apparatus and chlorophyll breakdown, which is indicated by low maximum photochemical efficiency of PSII in the dark-adapted state (Juvany et al., 2013). The complete dismantling of chloroplasts during leaf senescence generates nonphotosynthetic gerontoplasts (Fig. 1A). This process involves increased ROS production and a massive degradation of macromolecules by proteolysis and autophagy, remobilizing nutrients from leaves to other plant organs, mainly flowers and fruits (Gregersen et al., 2008; Guiboileau et al., 2013).

The corollas of many flowering plants and the exocarp of most fruits exhibit green colors at very early developmental stages. This green color is related to the presence of chlorophyll in the chloroplasts, which have

been shown to be photosynthetically active in several types of flowers and fruits such as petunias, lilies, orchids, apples (*Malus domestica*), strawberries (*Fragaria* spp.), and tomatoes (*Solanum lycopersicum*; Weiss et al., 1990; Blanke, 2002; Juneau et al., 2002; He and Woon, 2008; Cocaliadis et al., 2014; Naschitz et al., 2015). The yellow and orange colors acquired by flowers and fruits are due to carotenoids, a well-known group of lipophilic pigments that accumulate in chromoplasts (Fig. 1, B and C). In chromoplasts, carotenoids accumulate in large quantities in a wide range of lipid-associated proteins (PAPs) that determine chromoplast morphology (Ytterberg et al., 2006). Chloroplast differentiation into chromoplast starts with chlorophyll degradation and the disassembly of grana and thylakoids, which is similar to the process that occurs during chloroplast differentiation into gerontoplasts in senescing leaves. However, for the chloroplast-to-chromoplast transition, there is not a massive loss in the plastome, and sugars are imported from the cytosol to the chromoplast to sustain biosynthetic activities. Anthocyanins contribute to the red, purple, and blue colors of flowers and fruits. In contrast to carotenoids, large amounts of anthocyanins accumulate in vacuoles, giving rise to a number of colors depending on their chemical nature and vacuolar pH (Jaakola, 2013). Whitish flowers and fruits occur when chlorophylls have already degraded and carotenoids and/or anthocyanins are not (or are no longer) present, such as in senescing lilies (Fig. 1C).

A lot of attention has been paid to the biosynthetic mechanisms underlying carotenoid accumulation in the chromoplasts of flowers (Kishimoto and Ohmiya, 2006; Chiou et al., 2010) and fruits (Fraser et al., 1994; Kato et al., 2004; Fu et al., 2016), mainly because of consumer tastes. Moreover, there have been several projects to enhance carotenoid accumulation in food products by genetic engineering to overcome typical dietary diseases associated with carotenoid deficiency in developing countries (Ye et al., 2000; Diretto et al., 2007). However, little is known about the chloroplast-to-chromoplast transition, and only some genes have been identified as regulating this process in studies using the *Orange* cauliflower (*Brassica oleracea botrytis*) mutant, which has altered chromoplast biogenesis (Paolillo et al., 2004; Lu et al., 2006), and the *high pigment* mutant lines of tomatoes, which show altered chromoplast number and size (Mustilli et al., 1999; Cookson et al., 2003). Chromoplast generation not only strongly depends on carotenoid accumulation, which is influenced by ROS production (Pan et al., 2009), but also is influenced by N availability, sugar accumulation, and phytohormones such as GAs, cytokinins, abscisic acid, and ethylene (Iglesias et al., 2001). Regreening of tissues occurs in some leaves, flowers, and fruits when gerontoplasts or chromoplasts become active chloroplasts in the increased presence of GAs and/or cytokinins and a nitrate source (Goldschmidt, 1988; Zavaleta-Mancera et al., 1999; Prebeg et al., 2008). In chloroplast regeneration, the thylakoid system is restored from the invagination of the inner membrane of chromoplasts or membrane-bound



Figure 1. Comparative visualization of leaf, fruit, and flower development. A, *Arabidopsis* leaves experience leaf senescence during the mature stage, thus leading to the conversion of chloroplasts to gerontoplasts. B, Citrus fruits show a gradual shift from chloroplasts to chromoplasts in the exocarp, which mark the change in color from green to orange. C, Flowers also show characteristic color changes due to the conversion of chloroplasts to chromoplasts, such as tepals of lilies (cv LA Courier). In this model, however, carotenoid-accumulating chromoplasts, which can be observed at anthesis, are lost during senescence.

bodies, as described for cucumbers (*Cucumis sativus*; Prebeg et al., 2008). Although postharvest regreening of some types of flowers and fruits is regarded as negative because of the loss in quality (Hsu et al., 1989; Chen et al., 2013), there is a huge potential for chloroplast regeneration in planta at the intermediate stages of flower and fruit development in agri-food biotechnology. Delaying flower senescence and fruit ripening before harvest could enhance postharvest life and increase size and organoleptic properties by inducing higher photoassimilate production during the green stages and activating redox mechanisms to improve the antioxidant content, as has been shown for some fruits (Cocaliadis et al., 2014; Rademacher, 2015) and flowers (Arrom and Munné-Bosch, 2012; Imsabai and van Doorn, 2013). Degreening and regreening are indeed applied in some cases to increase market sales, such as for citrus fruits (Box 2).

PHOTOOXIDATIVE STRESS IN LEAVES, FLOWERS, AND FRUITS

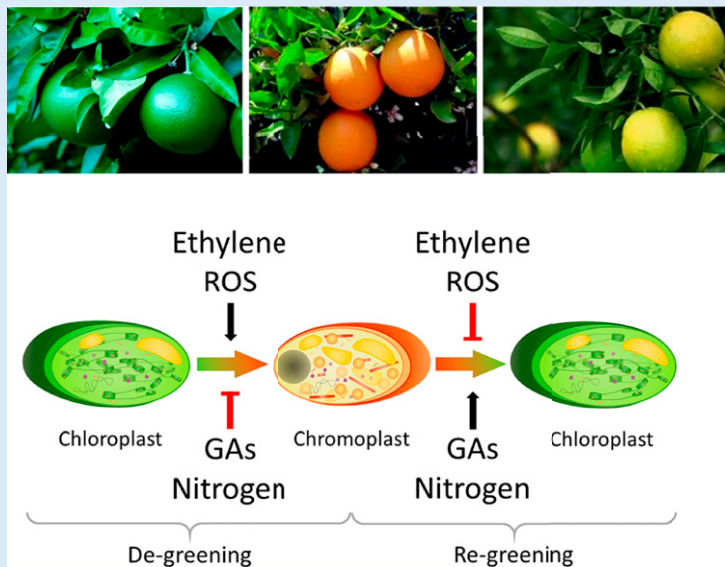
Oxygen was a key factor in promoting aerobic metabolism on Earth, supplying enough power to develop

complex structures such as the eukaryotic organisms we know today. However, the establishment of aerobic metabolism inevitably led to the production of ROS. In plant cells, ROS are generated mainly in four cellular locations: chloroplasts, peroxisomes, mitochondria, and the apoplast (Apel and Hirt, 2004). In leaves, the excessive energy in chloroplasts can be dissipated as thermal energy in nonphotochemical quenching or used to produce triple-state chlorophylls in the antenna and at the reaction center of PSII. Subsequently, triple-state chlorophyll activates oxygen, leading to the production of $^1\text{O}_2$, a highly unstable ROS. Superoxide anions ($\text{O}_2^{\cdot-}$) also can be produced by the direct reduction of oxygen in PSI (Mehler reaction) due to the absence of electron acceptors like ferredoxin or NADP^+ . $\text{O}_2^{\cdot-}$ is then converted rapidly by superoxide dismutase (SOD) into H_2O_2 , which is a more stable ROS, although hydroxyl radicals ($\text{OH}^{\cdot-}$), the most short-lived ROS, can be produced from H_2O_2 through the Fenton and Haber-Weiss reactions (Fig. 2A; Anthony et al., 2005; Asada, 2006; Pintó-Marijuan and Munné-Bosch, 2014). ROS have harmful effects on lipid peroxidation as well as on carbohydrate, protein, and DNA oxidation, leading to

BOX 2. Degreening and Regreening in Fruits

Degreening of fruits, such as oranges, is used as a postharvest treatment to accelerate marketing. Treatment of fruits at stage BBCH79 (see fig. below) with ethylene-releasing compounds accelerates chlorophyll degradation and makes it visually identical to ripen oranges. Although these fruits are not as good organoleptically as fruits that have ripened on the tree, they find a good price on the market.

Regreening of oranges and other fruits on the tree can be used as an effective means to prevent ripening and, when applied to late-ripe varieties, such as Lane Late (in the case of sweet oranges), can delay harvest and increase the period of oranges in the market (see fig. below).



programmed cell death during ROS overproduction (Gill and Tuteja, 2010). However, under redox homeostasis, there is a balance between ROS production and its detoxification by both enzymatic and nonenzymatic antioxidants (Foyer and Noctor, 2005a; Juvany et al., 2013). Antioxidants determine the duration and location of specific ROS, thus eliciting different signaling responses. 1O_2 has been described as a short-lasting ROS because it has a lifetime of approximately 4 μs and can diffuse relatively short distances (it can only travel around 200 nm, but chloroplasts are around 5–10 μm wide; Gill and Tuteja, 2010; Ogilby, 2010). Carotenoids, specifically β -carotene, tocopherols, and plastoquinone, are the main antioxidants triggering 1O_2 detoxification by (physical) quenching or (chemical) scavenging (Miret and Munné-Bosch, 2015). *Arabidopsis* (*Arabidopsis thaliana*) *fluorescent (flu)* mutants accumulate large amounts of chlorophyll precursors, including protochlorophyllide, in the dark and produce large amounts of 1O_2 when

illuminated (Meskauskiene et al., 2001). Illumination of these mutants for 15 min after a period of darkness has been shown to activate a distinct set of genes as a result of 1O_2 production in chloroplasts, showing the relevance of lifetime and site production on ROS signaling (op den Camp et al., 2003). In contrast to 1O_2 , H_2O_2 can be produced in different compartments in plant cells and is a more stable ROS with higher diffusion distances of around 1 μm (Vestergaard et al., 2012), thus with the potential of being able to diffuse from chloroplasts to nuclei to modulate gene expression (Exposito-Rodriguez et al., 2017). The AsA-glutathione cycle plays a major role in H_2O_2 detoxification in the water-water cycle. When H_2O_2 is produced, it is converted rapidly by ascorbate peroxidase into water and monodehydroascorbate (MDA). MDA is reduced subsequently to AsA by reduced ferredoxin or MDA reductase. Provided that MDA is not reduced directly to AsA, it spontaneously converts into AsA and dehydroascorbate,

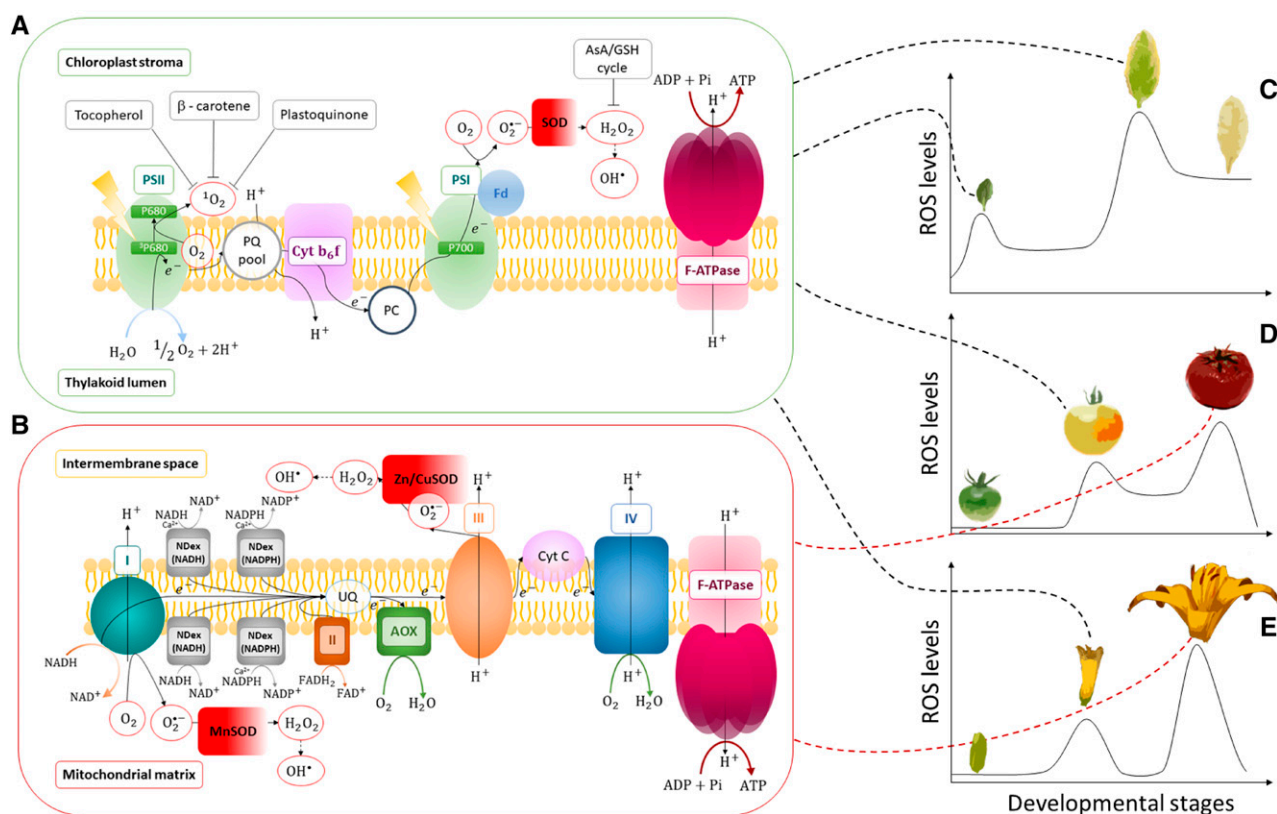


Figure 2. ROS production and temporal dynamics during organ development. A, Schematic representation of the chloroplast under excess light conditions. 1O_2 is produced in PSII when triple-state chlorophyll forms (3P680). Antioxidants like tocopherols, β -carotene, and plastoquinone can effectively eliminate 1O_2 . $O_2^{\bullet -}$ is produced through the direct reduction of oxygen in PSI (Mehler reaction) in the absence of electron acceptors like ferredoxin (Fd) or $NADP^+$, and it can convert into H_2O_2 by SOD. If H_2O_2 is not efficiently eliminated by the ascorbate/glutathione (AsA/GSH) cycle, it leads to the production of OH^{\bullet} in the Fenton and Haber-Weiss reactions. B, Schematic representation of a mitochondrion under oxidative stress. Complexes I and III are the main producers of $O_2^{\bullet -}$, which can be converted to H_2O_2 by MnSOD or Zn/CuSOD. C, D, and E, Simplified models for ROS production during leaf, fruit, and flower development, respectively. AOX, Alternative oxidase; Cyt b_6f , cytochrome b_6f complex; Cyt C, cytochrome c; NDex(NADH), external rotenone-insensitive NADH dehydrogenase; NDex(NADPH), external rotenone-insensitive NADPH dehydrogenase; NDin(NADH), internal rotenone-insensitive NADH dehydrogenase; NDin(NADPH) internal rotenone-insensitive NADPH dehydrogenase; PC, plastocyanin; PQ pool, plastoquinone pool; I, complex I (NADH:ubiquinone oxidoreductase); II, complex II (succinate dehydrogenase); III, complex III (cytochrome bc_1 complex); IV, complex IV (cytochrome c oxidase).

which is further reduced by dehydroascorbate reductase into reduced glutathione (GSH), which is finally recovered by glutathione reductase (Asada, 2006).

In leaves, ROS are produced not only under environmental conditions that trigger photoinhibition and photooxidative stress in chloroplasts but also during the very early and late stages of leaf development (Juvany et al., 2013). Photooxidative stress occurs in senescing leaves as well as in very young leaves when the photosynthetic machinery is still under construction, the xanthophyll cycle-dependent energy dissipation mechanisms are still not fully operational, and ROS production is increased due to the excessive energy in chloroplasts (Fig. 2C; Szymańska and Kruk, 2008; Lepeduš et al., 2011; Juvany et al., 2012). The occurrence and intensity of the double peak in ROS production during leaf development strongly depend on the specific

patterns of leaf development in each plant species. For instance, species with folded leaves during the early stages of leaf development are not exposed to high levels of light and, therefore, do not suffer photooxidative stress. Leaf longevity and environmental conditions also affect the timing and intensity of the second ROS peak, which is typically associated with the start of leaf senescence (Zimmermann and Zentgraf, 2005; Juvany et al., 2013).

Petal senescence and fruit ripening share some similar morphological and biochemical processes with leaf senescence, like chloroplast disassembly and protein degradation. ROS are indeed involved in flower development and fruit ripening, with oxidative stress occurring not only in the mitochondria (Fig. 2B), due to protein carbonylation and the increased respiratory rate during ripening affecting the redox state once sugars

become a limiting factor (Qin et al., 2009a; Kan et al., 2010; Tian et al., 2013), but also in plastids during the chloroplast-to-chromoplast transition. H_2O_2 levels increase in the berry skin of grape (*Vitis vinifera* 'Pinot Noir') at the onset of ripening (veraison), when the most crucial events during berry ripening occur, including the change in color of the skin (Pilati et al., 2014). Studies on tomatoes also have revealed an elevation in H_2O_2 levels during changes in color of the skin (Jimenez et al., 2002; Kumar et al., 2016). It appears, therefore, that color break during ripening is associated with increased oxidative stress in ripening fruits that is linked to a respiratory burst in the mitochondria and enhanced ROS production during chromoplast generation, which is essential for carotenoid production (Bouvier et al., 1998). In postharvest fruits, ROS are one of the main factors causing fruit decay (Vicente et al., 2006; Pavez et al., 2013). As in leaves, fruits also show a double peak in ROS production during their development, the first peak occurring at the start of ripening and the second during overripening either at preharvest or postharvest (Fig. 2D). Flowers also show a double peak in ROS production during development, but the timing differs. H_2O_2 accumulation in daylily (*Heemerocallis* spp. hybrid) petals show a double oxidative burst (Fig. 2E), one at the time of flower bud opening, once chlorophylls have mostly been degraded, and the other at the start of flower senescence (Panavas and Rubinstein, 1998). Unfortunately, however, the effects of chloroplast-to-chromoplast differentiation and the spatiotemporal location of ROS production on flower development have not been investigated yet in detail, although it appears that light and photosynthetic electron transport promote anthocyanin synthesis, as seen in petunia, and, therefore, might be essential in triggering flower development (Weiss and Halevy, 1991).

Fruit sunburn, which is linked to photooxidative stress in several types of fruits, such as watermelons (*Citrullis vulgaris*), tomatoes, peppers (*Capsicum annuum*), cucumbers, apples, and strawberries, is still an important agronomic concern in the agri-food biotechnology industry. Three degrees of sunburn may occur: (1) photooxidative sunburn, in which fruits become photobleached by excessive levels of light (due to sudden changes in light conditions within the canopy); (2) sunburn browning, which is caused by changes in the light environment and enhanced temperatures and is associated with the severe degradation of chlorophylls and carotenoids; and (3) sunburn necrosis, which is associated with even higher temperatures that destroy tissues on the sun-exposed side of the fruit by causing a loss in cell integrity and cell leakage (Torres et al., 2006; Racsco and Schrader, 2012). Protection against sunburn includes developing sufficient leaf cover in the canopy to shade the fruit, activating the xanthophyll cycle-dependent excess energy dissipation system, and providing effective antioxidant protection through low-molecular-weight antioxidants, such as carotenoids, tocopherols, ascorbate, glutathione, and

flavonoids, and by effectively using the ascorbate-glutathione cycle and other enzymatic antioxidants (Torres et al., 2006; Chen et al., 2008; Zhang et al., 2015).

REDOX SIGNALING DURING LEAF, FLOWER, AND FRUIT DEVELOPMENT

Although ROS have been traditionally viewed as harmful molecules, they are currently considered essential signaling molecules that are involved in plant responses to abiotic and biotic stress, plant growth, and development. In this context, photooxidative stress in leaves, flowers, and fruits affects redox signaling through the specific oxidation of target and signaling molecules. Lipids and proteins are excellent targets mediating cellular responses to imbalances in the redox state in chloroplasts, as fatty acids and amino acids (specifically sulfur-containing amino acids like Cys, Tyr, Trp, and His) are very susceptible to oxidative modification (Foyer and Noctor, 2005b; Han, 2017). There is limited information on the molecular mechanisms underlying ROS retrograde signaling in the chloroplasts of leaves, flowers, and fruits, although transcriptomic and proteomic approaches performed in recent years have provided important data.

Some ROS, like 1O_2 and $OH\cdot$, have limited diffusion distances. Thus, mechanisms other than direct diffusion must exist for redox signaling from chloroplasts to the nucleus. By contrast, H_2O_2 is more stable and can diffuse directly from chloroplasts to the nuclei (Exposito-Rodriguez et al., 2017), thus influencing gene expression in the nuclei both directly and indirectly (Fig. 3). Glutathione is an important signaling molecule, acting as a buffer between ROS and Cys groups and inducing calcium (Ca^{2+}) release into the cytosol to mediate ROS retrograde signaling via MAPK pathways (Gómez et al., 2004; Ray et al., 2012). Moreover, ROS affects the production of phytohormones like ethylene, GAs, and jasmonates (Shumbe et al., 2016). Studies using mutants have been essential in determining the genetic modifications produced by ROS. The Arabidopsis *flu* mutant was described to produce 1O_2 in leaves when illuminated after a period of darkness because of an overproduction of protochlorophyllide in the dark (op de Camp et al., 2003). Wagner et al. (2004) found that *EX1* was responsible for programmed cell death in bleached seedlings and growth inhibition in Arabidopsis *flu* mutants, with the EX1 protein located at the grana margins of chloroplasts mediating responses to 1O_2 production (Wang et al., 2016). Moreover, a recent study performed in the Arabidopsis mutant *chlorina1* showed that programmed cell death induced by 1O_2 under high levels of light was mediated by *OX11* via an EX1-independent pathway (Shumbe et al., 2016). In that study, *oxi1* mutants showed increased salicylic acid production and decreased expression of the genes associated with GA, ethylene, and jasmonic acid biosynthesis. Jasmonic acid regulates programmed cell death, while its precursor, 12-*oxo*-phytodienoic acid, plays

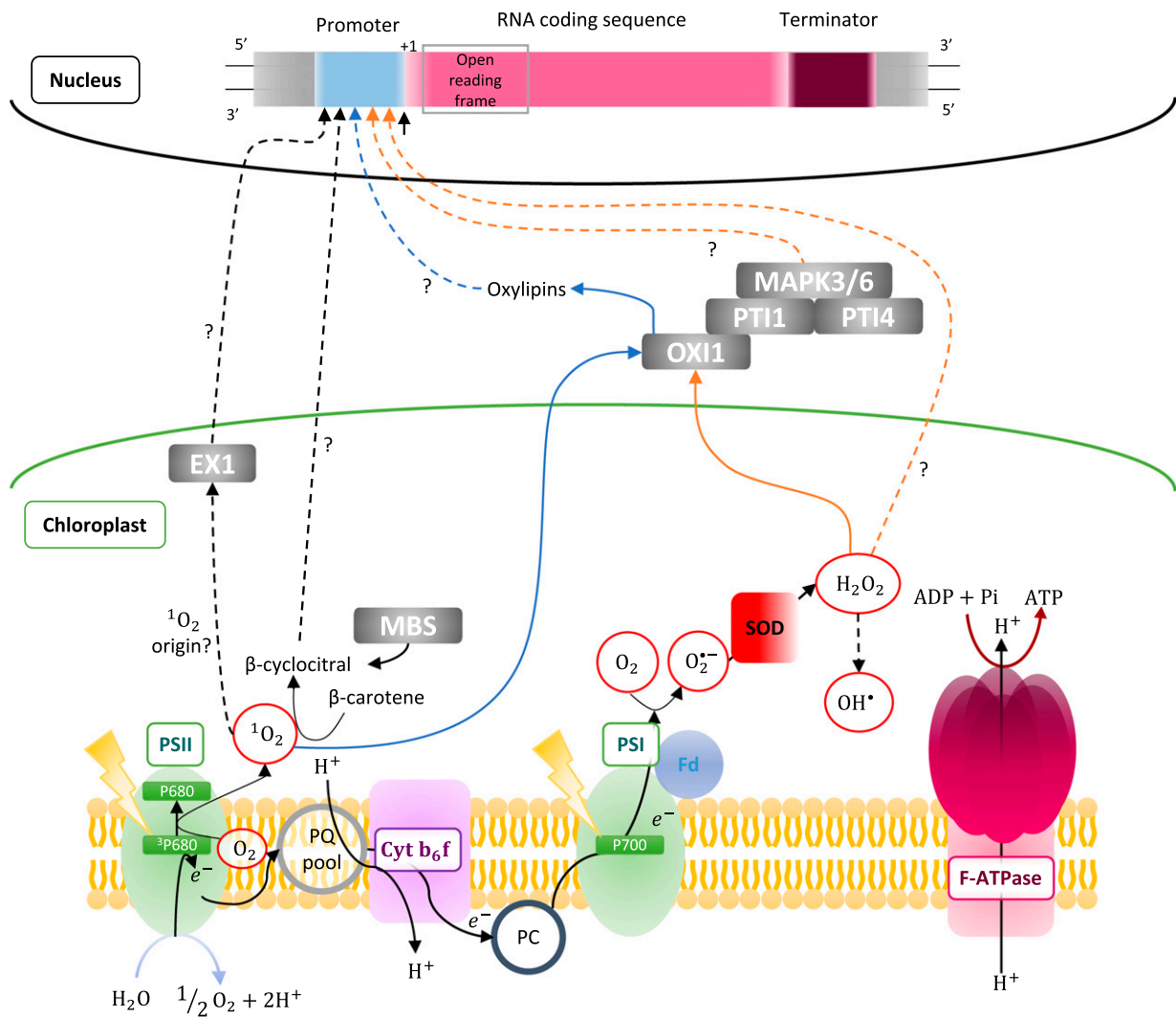


Figure 3. Retrograde signaling during photooxidative stress in chloroplasts. $^1\text{O}_2$ along with H_2O_2 have been described as signaling molecules able to modulate gene expression. EXECUTER1 (EX1) located at the grana margins has been reported to mediate responses to $^1\text{O}_2$ production, as well as OXIDATIVE SIGNAL INDUCIBLE1 (OXI1), which mediates $^1\text{O}_2$ response in an EX1-independent pathway, possibly through oxylipins. Moreover, oxidation products such as β -cyclocitral also are essential to mediate $^1\text{O}_2$ signaling. In contrast, H_2O_2 is a more stable form of ROS and direct modulation of gene expression could be possible, although this molecule also activates retrograde downstream signaling through mitogen-activated protein kinases (MAPK3/6) interacting with OXI1, protein kinase Pto-interacting1 (PTI1), and PTI4. Continuous lines show pathways and interactions already described in the literature, while discontinuous lines are unknown pathways. Cyt b_6f , Cytochrome b_6f complex; Fd, ferredoxin; MBS, METHYLENE BLUE SENSITIVITY; PC, plastocyanin; PQ pool, plastoquinone pool.

a major role in the acclimation process during photooxidative stress. Although H_2O_2 signaling transduces through the MAPK3 and MAPK6 signaling cascades activated by the complex of OXI1 with PTI1 and PTI4 (Rentel et al., 2004), $^1\text{O}_2$ does not appear to activate these signaling cascades, as *oxi1* mutants do not show any changes in the expression of genes encoding these proteins, indicating a different transduction pathway for OXI1 under $^1\text{O}_2$ regulation (Shumbe et al., 2016). Although $^1\text{O}_2$ signaling has been studied only in leaves thus far, the advent of molecular genetics in new models, such as tomatoes, paves the way for studying these signaling processes in both flowers and fruits. Indeed, carotenoid oxidation products

generated during $^1\text{O}_2$ scavenging, such as β -cyclocitral, also have been shown to be essential in transducing signals triggered by photooxidative stress and specific $^1\text{O}_2$ signatures (Ramel et al., 2012). Furthermore, a small zinc finger protein, MBS, is required to induce $^1\text{O}_2$ -dependent gene expression (Shao et al., 2013). Interestingly, however, *mbs1* mutants supplemented with β -cyclocitral are unable to positively regulate antioxidant-related genes that are usually activated in the wild type, in which the zinc finger transcription factor MBS1 is fully active and enhances plant tolerance to high levels of light (Shumbe et al., 2017). Lipids, rather than proteins, seem to be a target for oxidation in chromoplasts during the ripening of

OUTSTANDING QUESTIONS

- Mechanisms of retrograde signalling in flowers and fruits are still poorly understood. Do *EX1* and *OX11* genes play a role in flower and fruit programmed cell death?
- Do leaves, flowers, and fruits follow the same mechanisms for plastid differentiation? To what extent gerontoplasts in senescing leaves regulate cell death similarly to chromoplasts in flowers and fruits?
- How do leaves, flowers, and leaves finely regulate the threshold of ROS production to strictly regulate cell growth, differentiation, and death? Have these mechanisms been evolutionary conserved?

peppers (Martí et al., 2009), indicating that jasmonates are likely to play a major role in retrograde signaling as modulators of redox signaling during fruit ripening. This is consistent with the effects of jasmonates, particularly the free jasmonic acid form, on ethylene biosynthesis and color development in other fruits, such as apples and tomatoes (Fan et al., 1998). Furthermore, the activities of SOD and components of the AsA-GSH cycle are specifically up-regulated in chromoplasts during fruit ripening, thus suggesting that these enzymes may play a role in protecting plastids and could modulate signaling molecules such as $O_2^{\cdot-}$ and H_2O_2 (Martí et al., 2009). In addition to fruits, flower corollas also are an excellent model in which to study redox signaling triggered by photooxidative stress. In this regard, it is essential to consider the spatiotemporal accumulation of plant pigments during flower development. Carotenoid accumulation during the chloroplast-to-chromoplast transition implies a distinct photoprotective capacity of the organ compared with flowers accumulating anthocyanins in the vacuoles. Red, blue, purple, and yellow flowers all have completely different absorbance spectra that determine the extent of photooxidative stress in chloroplasts and redox retrograde signaling during flower development. Although still in its infancy, research in flower corollas already has shed some light on the regulation of developmental stages by chloroplasts. For instance, in petunia corollas, which accumulate large amounts of chlorophyll until flower opening, PSI appears to be more active than PSII in electron transport, and photosynthesis saturation occurs at low light intensities (Weiss et al., 1988). This might imply that chloroplasts in petunia corollas produce large amounts of ROS, eliciting retrograde signaling with specific H_2O_2 signatures. Interestingly, components of the PSI core complex have been shown to continue accumulating in

both petunia and carnation (*Dianthus caryophyllus*) corollas even after anthesis (Vainstein and Sharon, 1993), suggesting that specific redox signatures may regulate flower development that are not necessarily the same as those occurring in leaves. However, each plant species displays distinct pigmentation in flower corollas, which determines the extent of photoprotection and, therefore, the potential ROS signatures produced during flower development, an area that undoubtedly warrants further investigation.

CONCLUSION AND PROSPECTS

Molecular genetic studies have been pivotal in dissecting the key regulatory hubs in redox signaling. Flowers and fruits bearing chloroplasts during their early stages of development share some similarities with leaves but also important differences in terms of photosynthesis-derived ROS, the duration and extent of photooxidative stress, and redox signaling. Photooxidative stress may be considered a key effector of redox signaling during organ development, not only in leaves but also in some types of flowers and fruits. However, the unique patterns of pigmentation in flowers and fruits and the photosynthetic activity of fruit exocarps and flower corollas ultimately determine the specific redox signatures arising from chloroplasts. However, there are still many gaps in our knowledge on the redox mechanisms underlying flower and fruit development (see Outstanding Questions), and further research is needed to increase our understanding of flower and fruit development. This is not only essential for a better understanding of basic biology but also has important economic implications in the agri-food biotechnology sector.

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