



# Isoprenoids and phenylpropanoids are key components of the antioxidant defense system of plants facing severe excess light stress



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## ABSTRACT

Plants face excess light stress on daily as well as on seasonal basis. The excess of excitation energy on cellular organelles prone to reactive oxygen species (ROS) generation is further enhanced when plants growing in full sun concurrently experience drought and heat stress. These are the very conditions that promote the biosynthesis of a wide range of secondary metabolites. Plants display a highly integrated arsenal of ROS-detoxifying agents to keep ROS concentration under control for efficient signalling, while avoiding cell death. There is evidence that primary antioxidants, *i.e.*, antioxidant enzymes and low molecular-weight antioxidants, such as ascorbic acid and glutathione, are depleted under a severe excess of radiant energy. Here we discuss about how relevant secondary metabolites, namely isoprene, carotenoids, and flavonoids may complement the function of primary antioxidants to avoid irreversible oxidative damage, when plants experience intense, even transient stress events. We offer evidence of how plants orchestrate daily the antioxidant machinery, when challenged against multiple environmental stresses. It is indeed conceivable that daily variations in sunlight irradiance and air temperature may greatly alter the effectiveness of primary and secondary ROS-detoxifying agents. Finally, we discuss about the possible inter-relation between isoprenoid and flavonoid metabolism in plants facing high light coupled with drought and heat stress, as a consequence of severe stress-induced redox imbalance.

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## 1. Introduction

Plants routinely face a wide range of stress events, which fluctuate on daily as well as on seasonal basis. The inevitable consequence of living in an oxygen-rich environment when combined with environmental constraints is the accelerate production of reactive oxygen species (ROS), such as hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), singlet oxygen (<sup>1</sup>O<sub>2</sub>), superoxide anion (O<sub>2</sub><sup>•-</sup>), and hydroxyl radical (<sup>•</sup>OH). Plants, as sessile organisms, have imperatively evolved a multiplicity of well-coordinated “defence” systems, aimed to maintain sub-lethal levels of ROS while taking further advantage from their abilities to signal stressful conditions (Mittler *et al.*, 2004; Foyer and Noctor, 2012, 2013). In plant cells, ROS are produced as by-products of plant metabolism in

chloroplasts, mitochondria, and peroxisomes as well as in the apoplast by the action of NADPH-oxidase (Mittler, 2002; Mittler *et al.*, 2004; Apel and Hirt 2004; Maruta *et al.*, 2012). There is clear evidence that ROS (as well as ROS-induced changes in the ratio of oxidized to reduced forms of low molecular weight antioxidants, *i.e.*, redox couples, *sensu* Foyer and Noctor (2015)), constitute an important hub capable of fine tuning cell metabolism by ‘transmitting’ environment-induced perturbations, rather than representing dangerous by-products of aerobic metabolism (Foyer and Noctor, 2012).

For example, H<sub>2</sub>O<sub>2</sub>, due to its relatively long life-time and affinity for water channels (Bienert *et al.*, 2006, 2007) is a perfect signal transducing molecule in plants growing under both ‘optimal’ and stress conditions (Pastori and Foyer, 2002). H<sub>2</sub>O<sub>2</sub> may indeed mediate developmental processes because of its ability to activate mitogen activated protein kinases (MAPK)-induced signalling cascade (Kovtun *et al.*, 2000; Foreman *et al.*, 2003; Barba-Espín *et al.*, 2011), and stress-induced H<sub>2</sub>O<sub>2</sub> over production

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represents a local and systemic signal that allows plants to acclimate to different stress agents (Foyer et al., 1997; Rodriguez et al., 2002; Maruta et al., 2012). Even extremely reactive forms of oxygen, such as singlet oxygen ( $^1\text{O}_2$ ) and  $^1\text{O}_2$ -generated oxylipins have also been involved in the retrograde signalling from chloroplast to the nucleus, thus tightly controlling cell metabolism (Wagner et al., 2004; Fischer et al., 2007; Kim et al., 2008). Changes in the concentration as well as in redox state of major low-molecular weight antioxidants, i.e., ascorbic acid and glutathione, represent systemic signals that profoundly alter cell metabolism conferring further resistance to over production of ROS (Schnaubelt et al., 2015). Nonetheless, the extent to which external perturbations enhance ROS generation and their successive diffusion from photosynthetic organs may result in severe cellular damage up to include programmed cell death (Van Breusegem and Dat 2006; De Pinto et al., 2012). Therefore, plants have to make great efforts to finely tune ROS-derived signalling (preventing massive ROS generation and detoxify ROS once they are formed), when their capacity to use radiant energy to photosynthesis is severely constrained.

Main components of the antioxidant machinery of plants are low molecular-weight antioxidant metabolites and enzymes. These include ascorbate (ASA), glutathione (GSH), superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), and constitute the first line of defence against oxidative stress that operates in cellular compartments in which photosynthesis and photorespiration take place (Apel and Hirt, 2004; Foyer and Shigeoka, 2011; Noctor et al., 2014). However, stress-induced enhancement in the first line of antioxidant defence is not a general rule. The activity of antioxidant enzymes increases in stress-tolerant species or genotypes, but may decrease steeply in stress-sensitive counterparts (Schwanz and Polle, 2001; Hernández and Almansa, 2002; Hernández et al., 2003). This simply means that primary antioxidants may be depleted depending on stress severity (Fini et al., 2011). Sensitivity to multifarious stressors is generally estimated in terms of a plant's ability to fix carbon and hence to promote new growth. It is therefore conceivable that the extent to which radiant energy reaching the photosynthetic apparatus exceeds the plant ability to use it to photosynthesis because of environmental stressors, may profoundly affect the effectiveness of primary ROS detoxifying agents (Fini et al., 2012, 2014). In other words, exposure to excess light stress may result into transient activation/inactivation of antioxidant enzyme activities (Polle, 2001; Mullineaux and Karpinski 2002; Mubarakshina et al., 2010; Fini et al., 2011, 2014).

Plants have evolved a variety of additional antioxidant systems, which are indeed activated in response to severe excess of sunlight irradiance (Agati et al., 2012, 2013; Esteban et al., 2015). Secondary metabolites are well suited to constitute a 'secondary' antioxidant system to transiently complement the action of primary antioxidants, as secondary metabolite biosynthesis is mostly activated in response to a severe excess of radiant energy (e.g., because of changes in the redox state of the cell, Agati et al. (2012, 2013)), see below Section 5 for details). The cost, in terms of energy and carbon, for secondary metabolites biosynthesis is balanced by the multiplicity of functions that secondary metabolites may serve in plants suffering from severe excess light stress (Loreto and Schnitzler, 2010; Agati and Tattini, 2010). Non-volatile isoprenoids, such as carotenoids, and flavonoids have the ability to avoid ROS generation as well as to counter ROS-induced damage (see next sections for details). In other words, they are potent antioxidants, following authoritative definitions given by Halliwell and Gutteridge (1989) and Halliwell (2009).

Here we explore the issue of how plants may orchestrate key components of the antioxidant machinery when severely stressed by an excess of radiant energy. In particular, our focus is on

isoprenoids and flavonoids, and we discuss about the potential of this vast class of secondary metabolites to complement the functions of primary antioxidants in plants facing concurrently exposed to multiple stress agents. The matter has outstanding ecological significance for plants inhabiting most areas worldwide, particularly the arid and semi-arid regions, as the frequency of intense stress events, such as scarcity of rainfall coupled with heat waves, is predicted to increase in the next future because of climate change (Mateasanz and Valladares, 2014; Tattini and Loreto, 2014).

## 2. Primary antioxidant defences decline under severe excess light stress

There is compelling evidence that enzymes aimed ROS detoxification decline in leaves, in which excitation energy to the chloroplast is in great excess (Casano et al., 1997; Streb et al., 1997; Polle, 2001; Mullineaux and Karpinski, 2002). This poses some concerns whether antioxidant enzymes constitute an efficient control system against stress induced ROS production (Peltzer and Polle, 2001; Peltzer et al., 2002; Apel and Hirt, 2004; Schützendübel et al., 2001; Fini et al., 2012, 2014). APX and CAT are depleted in plants exposed to severe excess excitation energy (Polle, 2001; Mullineaux and Karpinsky, 2002; Hatier and Gould, 2008; Mubarakshina et al., 2010; Agati et al., 2012) especially when other environmental constraints concurrently reduce the use of light energy for carbon fixation (Fini et al., 2011, 2012). There is evidence that APX activity is particularly sensitive to high temperature and sunlight irradiance (De la Haba et al., 2014) as revealed by both *in situ* and *in vitro* analysis of enzyme activity (Peltzer and Polle, 2001; Peltzer et al., 2002). Temperature dependent reduction of enzyme activities may be further enhanced under severe drought induced limitations of photosynthesis, which in turn contribute forming excess excitation energy (Fini et al., 2011, 2012).

Similarly to antioxidant enzymes, also the concentration of ASA and GSH generally increases under mild to moderate stress, but may decrease when the stress become more severe, in concomitance with severe limitation of photosynthesis (Herbinger et al., 2002; Guo et al., 2006; Zechmann et al., 2011; Koffler et al., 2014). Notably, drought induced decrease in ascorbate and glutathione concentrations in *Arabidopsis* was mostly due to depletion in chloroplasts and peroxisomes, whereas the concentration of vacuolar ASA steeply increased (Koffler et al., 2014). It was suggested that ASA may have a role as  $\text{H}_2\text{O}_2$  – detoxifying in the vacuole (Koffler et al., 2014), possibly behaving as a 'secondary vacuolar antioxidant', as detailed below in Section 4.

The extent of stress-induced depletion of primary antioxidant defences determine cell and whole-organ fate. Indeed, ROS may represent an unsolvable dead threat for the cell or instead activate a network of defences (through ROS-signalling) conferring further stress tolerance (Suzuki and Mittler, 2012; de Dios Barajas-López et al., 2013; Van Breusegem and Dat, 2006) in a very narrow concentration range (Cheeseman, 2006). The matter needs further investigations, examining the responses of plants to multiple stressors on long-term basis.

## 3. Antioxidant functions of volatile and non-volatile isoprenoids in high light-stressed leaves

As mentioned above, the conditions that lead to depletion of primary antioxidants can activate the biosynthesis of relevant secondary metabolites. This is exactly the case of volatile (here the discussion is centred on isoprene, the functions of which have been deeply explored) and non-volatile isoprenoids (Esteban et al., 2015; Rasulov et al., 2014). These metabolites are therefore best suited to complement the function of primary chloroplast

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