



Multiple functions of polyphenols in plants inhabiting unfavorable Mediterranean areas



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ABSTRACT

The significance of polyphenols, with emphasis to flavonoids, in the responses of Mediterranean plants to unfavorable environments, is discussed based on their ability to serve multiple functions in plant–environment interactions. Plants challenged against multiple stressors, as usually occurs in the Mediterranean basin, make a great investment in the biosynthesis of carbon-based-secondary-compounds, i.e., defense compounds *sensu lato*. Polyphenols are probably the most versatile secondary metabolites, thus allowing plants to respond promptly to unpredictable stress agents of different origin. Each individual species indeed displays a rich arsenal of polyphenol structures, which have different inter- and intra-cellular distribution. This review article is centered on the functions of polyphenols, particularly flavonoids as UV-screening, antioxidant and developmental regulators, and the relative significance of these roles in the acclimation/adaptation of plants to severe constrains of the Mediterranean climate. Here we suggest that flavonoids serve major roles as antioxidants rather than UV-screening pigments in Mediterranean plants challenged against an excess of sunlight irradiance. Furthermore, we discuss about the potential of flavonoids, particularly antioxidant flavones and flavonols, to regulate the development of organs and the whole plant. This ability may have great value for the ecology of plants inhabiting unfavorable Mediterranean environments, but this matter needs further investigation.

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1. Introduction

Plants in their natural habitats are exposed to multiple, frequently interactive stress factors, most of which are becoming more severe due to global change (Valladares et al., 2008). Global climate change imposes to Mediterranean regions a general increase of temperatures and aridity, coupled with a higher frequency of extreme climatic events such as heat waves and late-winter frosts (Diffenbaugh et al., 2005; Christensen et al., 2007). This represents a complex challenge for plants inhabiting Mediterranean-type ecosystems (Valladares et al., 2008). Plants suffering from more than one extreme stress event in a single growing season (Wollenweber et al., 2005), mobilize the “whole” metabolic machinery toward plant acclimation and survival (Chaves et al., 2010), thus allowing their persistence in harsh environments (García and Zamora, 2003). This ‘metabolic plasticity’ is costly, as fresh assimilated carbon and energy are diverted from growth, but may represent a key determinant for the survival of

plants in the harsh Mediterranean environment (Pearse and Hipp, 2012).

Mediterranean plants experience high sunlight irradiance most of the year, which translates, in many instances, in severe excess light stress. Drought/salinity and hot temperatures indeed strongly limit the use of radiant energy for CO₂ fixation (Chaves et al., 2009). Limitation to net CO₂ assimilation also occurs due to the scarcity of soil nutrients in most Mediterranean areas (Aerts, 1995). Mediterranean species, particularly woody evergreens make a great investment in the biosynthesis of carbon-based-secondary-compounds, i.e., defense compounds *sensu lato*, rather than investing in nitrogen-based compound biosynthesis (Stamp, 2003; Tharayil et al., 2011; Pearse and Hipp, 2012). Secondary metabolites may have, therefore, a central role in the strategies adopted by plants to cope with the Mediterranean climate (Kutchan and Dixon, 2005; Pollastri and Tattini, 2011), thus significantly contributing to phenotypic plasticity (Tattini et al., 2005, 2006).

Secondary metabolites indeed serve more than one function in response to severe environmental constraints (Dixon and Paiva, 1995; Vickers et al., 2009; Agati and Tattini, 2010; Ramel et al., 2012). Plants ‘waste’ considerable amounts of photosynthetic carbon for isoprene biosynthesis instead of fixing it into carbohydrates (Loreto and Schnitzler, 2010). Isoprene biosynthesis is still

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significant when photosynthesis steeply declines under severe drought, as isoprene biosynthesis is sustained by other carbon sources (Brilli et al., 2007). This massive use of both newly-assimilated and stored carbon for isoprene biosynthesis equips leaves with a versatile metabolite, which enhances the integrity of thylakoid membranes (Singsaas et al., 1997; Velikova et al., 2011), scavenges reactive oxygen (ROS) and nitrogen (RNS) species (Velikova et al., 2005; Vickers et al., 2009), and mirrors an enhanced biosynthesis of ABA (Barta and Loreto, 2006). Similarly, carotenoids behave as physical and chemical quenchers of singlet oxygen ($^1\text{O}_2$, Ramel et al., 2012), greatly affect physical properties of thylakoid membranes, other than contributing to thermal dissipation of excess excitation energy to PSII through nonphotochemical quenching (NPQ). β -Carotene or zeaxanthin either decrease or increase membrane rigidity, thus offering protection to the chloroplast against freeze or drought stress, respectively (Du et al., 2010). High sunlight- or drought-induced increase in zeaxanthin biosynthesis in some Mediterranean species only in part contributes to NPQ (Melgar et al., 2009; Remorini et al., 2009; Guidi et al., 2010; Fini et al., 2012), thus countering $^1\text{O}_2$ -induced damage to chloroplast membranes rather than merely avoiding $^1\text{O}_2$ generation (Havaux et al., 2007).

Polyphenols have likely the greatest ability to serve multiple functions in plants exposed to a wide range of abiotic stresses (Agati et al., 2012, 2013). Huge amounts of phenolic structures, distributed in different organs, cells and sub-cellular compartments are indeed present in each individual species (for a recent review, see Agati et al., 2012). This review article is centered on the functional roles of cell-located polyphenols, but cell wall-conjugated polyphenols may serve functions of great value in Mediterranean plants exposed to different stressors (Bussotti et al., 1998; Reig-Armiñana et al., 2004; De Micco and Aronne, 2012). Polyphenols, such as phenolic glucosides, hydroxycinnamic acid derivatives and flavonoids are involved in secondary cell wall thickening (Gunnaiyah et al., 2012), thus mechanically increasing reinforcement of tissues, a key anatomical feature conferring drought tolerance. Furthermore, polyphenol-induced strengthening of cell wall coupled with chemical-related functions (Gunnaiyah et al., 2012), may also enhance resistance to oxidative stress of both abiotic and biotic origin (Bennet et al., 1996; McLusky et al., 1999; Agati et al., 2012).

It has been recently shown that the biosynthesis of polyphenols increases steeply in plants in response to high sunlight in the absence of UV-irradiance or following nitrogen/water deprivation, heat/cold and root zone salinity (for reviews, see Lillo et al., 2008; Jaakola and Hohtola, 2010; Agati et al., 2012; Fini et al., 2011; Di Ferdinando et al., 2012). This suggests for polyphenols, particularly flavonoids vastly different functions in plant-environment interactions, possibly linked to abiotic stress-induced generation of ROS (Agati and Tattini, 2010). In turn, polyphenols also enhance plant defense to biotic stressors (Close and McArthur, 2002; Eyles et al., 2010).

Although ROS generation is the inevitable consequence for organism living in O_2 -rich environments, oxidative stress may be particularly severe for plants inhabiting Mediterranean regions. Polyphenols, as most other secondary metabolites, function at avoiding the generation of ROS and then quench ROS once they are formed (Agati and Tattini, 2010). Polyphenols may act as screeners not only of UV-radiation but also of short-wave visible radiation (e.g., ellagitannins and anthocyanins, Manetas, 2006; Tattini et al., 2007; Hatier and Gould, 2008). Polyphenol biosynthesis safely dissipate an excess of radiant energy and photo-assimilates for their biosynthesis (Hernández and Van Breusegem, 2010), although this 'function' does not exclusively involve polyphenols (and unlikely of primary significance). Polyphenols, particularly the structures with a catechol group in the benzene ring, are effective in complexing

metal ions (Agati et al., 2012) that are responsible for the generation of extraordinarily reactive free radicals, such as the hydroxyl radical in the presence of hydrogen peroxide (H_2O_2) (Fenton reaction, see Hernández et al., 2009). Flavonoids (e.g., the dihydroxy B-ring-substituted forms) have the ability to preserve chloroplast envelope membranes from photo-oxidation by interacting with membrane phospholipids (Erlejman et al., 2004; Scheidt et al., 2004; Agati et al., 2013) as well as by chemically quenching $^1\text{O}_2$ (Agati et al., 2007). Finally, vacuolar located polyphenols (e.g., caffeic acid derivatives, quercetin derivatives, anthocyanins) may reduce hydrogen peroxide (H_2O_2) which is supposed to diffuse out of the chloroplast to the vacuole under excess light stress conditions (Agati et al., 2007, 2013; Ferreres et al., 2011). It is worth noting that the vacuole does not possess an effective antioxidant defense system (Agati et al., 2013): e.g., ascorbic acid is not a good substrate for vacuolar peroxidases (POX, Sakihama et al., 2000). Therefore, vacuolar-located flavonoids may constitute a H_2O_2 detoxifying system (in conjunction with POX) of primary significance in plants suffering from severe excess light stress, when the activity of primary antioxidant defenses steeply declines (for a review, see Agati et al., 2013). Recent evidence suggests for polyphenols, particularly flavonoids (including anthocyanins) a major role as developmental regulators/signaling molecules (Taylor and Grotewold, 2005; Peer and Murphy, 2006; Hatier and Gould, 2008; Pollastri and Tattini, 2011; Agati et al., 2012). Flavonoids may indeed contribute to morpho-anatomical adjustments of plants challenged against a wide array of abiotic stresses (see Section 3.3; Potters et al., 2007; Agati and Tattini, 2010; Agati et al., 2013; Buer et al., 2013).

Here, we focus our attention on the multiple functions potentially served by polyphenols, with special emphasis to UV-B-absorbing flavonoids (anthocyanins will be marginally considered here, but please refer to excellent papers by Kytridis and Manetas, 2006; Manetas, 2006; Chaves et al., 2010 for details) in the responses of plants to excess light stress, a primary challenge Mediterranean species face on a daily and a seasonal basis.

2. Do polyphenols contribute to species richness in unfavorable Mediterranean ecosystems?

Co-occurring Mediterranean species display very contrasting polyphenol composition and concentration (Tattini et al., 2000, 2006, 2007; Romani et al., 2002), thus suggesting for polyphenols multiple and species-specific functions in plants inhabiting severely constrained Mediterranean regions. Here we present a study-case of three species, which co-occur on Mediterranean sea-shore dunes, *Phillyrea latifolia*, *Pistacia lentiscus*, and *Cistus* spp. (*Cistus salvifolius* and *Cistus incanus*, Fig. 1), to elucidate the multiplicity of roles played by polyphenols in species-specific mechanisms of adaptation to an excess of sunlight radiation.

P. latifolia and *P. lentiscus* are woody evergreen sclerophylls, whose leaf longevity largely exceeds that of *C. salvifolius*/*C. incanus* (Brosse, 1979), which are semi-deciduous species that may display seasonal dimorphism because of dry summer (Aronne and De Micco, 2001). *P. latifolia* and *P. lentiscus* display very thick (approximately 500- μm -thick; Fig. 1A and C) and coriaceous leaves at the sunny sites, whereas *Cistus* leaves are soft and thin (<250 μm -thick, Tattini et al., 2007; Fig. 1B). Cuticle thickness ranges from approximately 12–15 μm in *P. latifolia* and *P. lentiscus* to 6–7 μm in *Cistus* spp. (Brosse, 1979, Fig. 1A–C). Fully developed leaves of *P. latifolia* had sparse (less than 10 mm^{-2} , Tattini et al., 2000) glandular, highly specialized secretory trichomes mostly distributed on the abaxial surface (which allows steeply angled sunny leaves to minimize light absorption during the midday hours, Vogelmann, 1993; Tattini et al., 2000). Instead, a dense indumentum of stellate and

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