



The importance of non-photosynthetic pigments and cinnamic acid derivatives in photoprotection

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Abstract

Excess light and UV-radiation are hazardous natural stress factors, and plants have evolved a range of avoidance and tolerance strategies employing versatile tools against these constraints. The paper outlines the contribution of non-photosynthetic pigments to the protection of plants from excess light and UV-radiation, as well as the mechanisms involved. A large pool of secondary metabolites, belonging mainly to the highly diversified array of flavonoids ($C_6-C_3-C_6$ types), and the closely related anthocyanins (flavylium salts, $C_6-C_3-C_6^+$ types), as well as betacyanins are often referred to as non-photosynthetic pigments. In addition to screening out incoming visible and UV-radiation by absorption, these pigments can dissipate excess photon energy, while the antioxidant and reactive oxygen species (ROS)-scavenging ability of non-photosynthetic pigments can also protect against light- and UV-induced oxidative stress. Their role in adjustment of source activity to reduced sink strength is examined as a possible mechanism of protection in conditions where excess light stress is aggravated by other constraints limiting the CO_2 assimilation. Evidence for the photoprotective role involving UV-screening, antioxidant activity, ROS-scavenging and energy-dissipation of another group of secondary metabolites, cinnamic acid derivatives (C_6-C_3 types), is also discussed.

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1. Introduction

Solar radiation is a prerequisite for life on Earth as a major source of energy driving the photosynthetic process. Excess light, however, is detrimental for plants, disturbing their development and decreasing their production. It generates a flux of excess electrons, leading to over-reduction of the electron

transport chains (ETC) and overproduction of NADPH. This may result in increased formation of harmful reactive oxygen species (ROS) in the ETC (Mehler reaction, generating $O_2^{\bullet-}$, which is then dismutated to H_2O_2), and damage the photosynthetic process. Overproduction of NADPH and decreased $NADP^+$ regeneration can interfere with normal functioning of the Calvin cycle (Vranova et al., 2002; Zhang et al., 2003). The input of excess light energy to O_2 can produce highly reactive singlet oxygen which has a strongly deleterious effect on

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chloroplast pigment–protein complexes (Foyer et al., 1994; Foyer and Noctor, 2000).

UV-radiation is a common component of the solar radiation, but high UV-fluxes that exceed the ecologically normal UV-levels to which living organisms are adapted can damage both animal and plant organisms. Molecules of high biological significance (nucleotides, nucleic acids, photosynthetic pigments, proteins) absorb highly energetic UV-B photons and thus become sensitive targets for UV-damage. Aromatic chemical groups in these molecules underly UV-B absorption. Moreover, noxious ROS result from these interactions (Greenberg et al., 1997; Galatro et al., 2001; Jansen, 2002; Stratmann, 2003; Barta et al., 2004). UV-radiation often acts synergistically with air pollution which results from the badly regulated human activities in a strongly industrialized society. For example, ozone, as a strong selective absorber of UV-B and -C rays, serves as a reliable shield in the stratospheric layers against these UV-rays. Unfortunately, due to pollution factors, stratospheric O₃ is increasingly depleted, giving rise to the so-called “ozone holes” allowing increased UV-B radiation to reach the Earth’s surface (Smith et al., 1992; McKenzie et al., 2003).

Plants have evolved a range of avoidance and tolerance strategies against excess light and UV-radiation (Jansen, 2002; Steyn et al., 2002). They employ morphological, histological and biochemical adaptations to avoid penetration of light and UV-rays into plant tissues. A large array of biochemical mechanisms are co-opted in tolerance responses, counteracting detrimental effects of absorbed light and UV, such as ROS generation and accumulation (Jansen, 2002; Semerdjieva et al., 2003; Stratmann, 2003). Moreover, an enzyme-assisted strategy to repair the UV-induced damage is operative in many plants (Waterworth et al., 2002).

Numerous studies on carotenoids using both molecular and ecophysiological approaches have demonstrated the photoprotective role of these photosynthetic pigments as structure-stabilising units of the light-harvesting complex, as essential components of the ROS-scavenging pool, and as constituents of the xanthophyll cycle, dissipating absorbed excess light energy as heat (Hirayama et al., 1994; Edge et al., 1997; Gonzalez-Rodrigues et al., 2001; Davison et al., 2002; Demmig-Adams, 2003; Müller-Moule et al.,

2003). Less research, however, has addressed the photoprotective functions of secondary metabolites related to the phenylpropanoid pathway: flavonoids and anthocyanins (referred to as non-photosynthetic pigments), and cinnamic acid derivatives. Photoprotective properties of these compounds can be inferred from their distinctive chemistry which suggests specific light absorption and antioxidant capacity. The present paper considers the evidence for a role in photoprotection of such non-photosynthetic pigments and cinnamic acid derivatives.

2. Chemical structure, properties, biosynthesis and localization of non-photosynthetic pigments and cinnamic acid derivatives

The pigments concerned are highly diversified and include flavonoids (C₆–C₃–C₆ types), the closely related anthocyanins (flavylium salts, C₆–C₃–C₆⁺ types) and betacyanins (nitrogen-containing red pigments) all of which absorb in the UV and blue to green regions of the visible, together with the cinnamic acid derivatives (CAD, C₆–C₃ types) which absorb only in UV. Such radiation absorption acts as a radiation screen and explains why they may be important in photoprotection (Dixon and Paiva, 1995; Greenberg et al., 1997). These compounds, widely distributed in plants, are less frequently present in a free form, occurring predominantly in a conjugated state: flavonoids, anthocyanins and betacyanins occur mainly as glycosides, and CAD – as esters, amides, depsides, etc. Conjugation, being an important mechanism to modulate toxicity, solubility and subcellular targeting of aglycones and free acids, contributes to the extraordinary variability in distribution, property and function patterns of free and conjugated types. Thus the presence of benzene ring in flavonoids, anthocyanins and CAD, as well as a short unsaturated hydrocarbon chain in the latter determines the low polarity and low water solubility of the free forms of these compounds. Glycosylation, esterification, amidation, hydroxylation, etc., enhance their polarity and water solubility, which may lead to a multiplicity of functional changes (Harborne, 1999). The structure of some mostly distributed representatives of the above-described groups of compounds is given in Fig. 1.

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