Plant Science 175 (2008) 449–458

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

Plant stress and human health: Do human consumers benefit from UV-B acclimated crops?

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ARTICLE INFO

Article history:
Received 8 January 2008
Received in revised form 29 April 2008
Accepted 29 April 2008
Available online 4 May 2008

Keywords:
Plant metabolite
UV-B radiation
Stress
Nutritional value
Metabolomics
Acclimation

ABSTRACT

Plants are sessile organisms, and consequently cannot avoid exposure to stressful environmental conditions. Exposure to mild stress conditions can induce active acclimation responses, while more severe conditions cause metabolic disruptions. A common plant acclimation response to a variety of environmental stressors is the accumulation of antioxidants and secondary metabolites. For example, ultraviolet-B (UV-B) radiation impacts on the levels of a broad range of metabolites, including phenolic, terpenoid and alkaloid compounds. Our survey of the literature reveals that the levels of some of these metabolites increase following UV-B exposure, while those of others decrease, change transiently or are differently affected by low and high UV-doses. This includes several compounds that are pharmacologically active and/or nutritionally important. We conclude that the complex patterns of stress-induced changes in plant metabolites need to be studied in more detail to determine impacts on the nutritional and pharmacological characteristics of food products. Claims that UV-B acclimated plants have nutritional benefits are currently unproven.

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Contents

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Abbreviations: Asc, L-Ascorbate; DHA, dehydroascorbate; GSH, glutathione; GSSG, glutathione disulfide; PAR, photosynthetically active radiation; ROS, reactive oxygen species; UV-B, ultraviolet-B.

0168-9452/$ – see front matter © 2008 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.plantsci.2008.04.010

1. Life is stressful for a plant

Plants are sessile organisms, and consequently, cannot avoid being exposed to unfavourable environmental conditions. Such exposure can lead to disruption of metabolic processes at the molecular, cellular, organismal or even ecosystem level, and this is typically referred to as plant ''stress'' [1]. Different stresses have different molecular targets in the cell. However, a common consequence of the exposure to many distinct types of unfavourable environmental conditions is the occurrence of oxidative stress, mediated by increased levels of ROS [2]. ROS are directly linked to oxidative damage to, among others, DNA, lipids, and proteins, as well as to cellular and intercellular signalling responses. Nevertheless, there is more to stress than just deleterious effects at the metabolic level (distress), and the focus in stress physiology has moved from how plants survive 'acute' (sudden and short-term) and 'sub-lethal' doses to how plants respond to 'chronic' (long-term), 'suboptimal' growing conditions. In parallel, the concept of stress has changed, defining stress as the impact of changing environmental conditions, often changing from one suboptimal condition to another, on plant growth and fitness. This concept of ''positive'' or eustress emphasises the high degree of plasticity possessed by plants, and the capability to adjust to changing environmental conditions by physiological state-changes [3] or genetic adaptation [4]. Acclimation is the physiological phenomenon that tolerance to stress increases following exposure to unfavourable environmental conditions. Acclimation responses have been characterised in considerable detail during the last 10 years, mainly via micro-array gene-expression analysis as well as increasingly via proteomic and metabolomic approaches.

The study of stress-induced responses is mainly driven by a desire to develop stress tolerant crop species, which require less input of resources and/or produce higher yields in stressful conditions. In comparison, little attention has been paid to the consequences of plant stress acclimation for the nutritional and/or pharmacological value of plant based materials. This is remarkable, considering that a range of environmental factors, including light, temperature, micro-organisms, and insects, nutrients and heavy metals impact on the metabolite composition of plants [3,5] and that many plant secondary metabolites are determinants of both plant stress tolerance [2] and nutritional value [6].

2. Plant stress responses and nutritional value

Exposure to a stress can impact on the nutritional properties of plant material. The most direct effect is when the stressor itself is passed on into the food chain. This scenario has been studied in detail for metals like cadmium, lead, zinc and copper, which can all, accumulate in plant tissues. More commonly, stress impacts on the levels of specific metabolites, which in turn can affect the nutritional value of plant tissues. An example of the intimate relation between plant stress and human nutrition is the biology of ascorbate. Plants are the main source of ascorbate (vitamin C), which is an essential nutrient for humans. In humans, a lack of vitamin C hampers the activity of a range of enzymes, and may lead to ''scurvy'' [7]. Ascorbate is also a central antioxidant in plant metabolism, and its involvement in stress responses has been extensively documented [2]. The relationship between plant stress acclimation and human health is not limited to antioxidants, but comprises a broad array of metabolites some of which possess ''desirable'' pharmacological properties. For example, hyperforin is an active ingredient in St. John's wort (*Hypericum perforatum*), and alleviates mild depression by inhibiting re-uptake of neurotransmitters [8]. Exposure of St. John's wort plants to heat stress substantially increases hyperforin concentration in shoots [9], thus increasing the efficacy of pharmacological extracts. Other stress-induced metabolites are toxic to humans. Glycoalkaloids such as α-solanine and α-chaconine accumulate in potato tubers that have been exposed to mechanical stress or light [10], and these compounds cause gastro-intestinal or neurological disorders in humans. Accumulation of these glycoalkaloids is directly associated with accumulation of phytosterols [11], which themselves have positive effects on human health and are increasingly used as nutraceuticals. Phytosterols limit absorption of cholesterol from fat matrices into the intestinal tract, which in turn results in lower cholesterol levels in human consumers and decreases the incidence of cardiovascular disease [12].

These examples demonstrate a link between stress-induced changes in metabolite levels and the nutritional and/or pharmacological value of plants. However, they also demonstrate that this link is complex, and that understanding control of metabolite accumulation is vital in order to recognise potential food safety issues, to improve the nutritional value of food, and to facilitate development of novel, biotechnological plant products, including human therapeutics and phytopharmaceuticals [13].

3. UV-B radiation as an environmental stressor

In this contribution, we will analyse metabolic responses following exposure of plants to one specific stressor, UV-B (280–315 nm) radiation, with an emphasis on plant secondary metabolites. UV-B wavelengths greater than 290 nm, are a ubiquitous component of solar radiation in the biosphere. Levels of UV-B in the biosphere vary quite considerably, both spatially and temporally. The UV-screening stratospheric ozone layer is relatively thin at low latitudes and this, in combination with a steep solar angle, results in relatively high UV-B levels in the tropics, compared to mid and high latitudes [14]. High levels of UV-B also occur at high altitudes. Such spatial variations in UV-B penetration are complemented by temporal variations, which are caused by changes in the position of the sun, as well as seasonal changes in thickness of the ozone layer and in general meteorological conditions [14]. During the last three-decades, average UV-B dose-rates in the biosphere have increased as a consequence of ozone-layer depletion by man-made halogenated chemicals, including chlorofluorocarbons. Increases in surface UV-B have been estimated to be in the range of 2–5% per decade for Central Europe [14]. The concentrations of major ozone-depleting substances in the atmosphere are currently decreasing, and recovery of the ozone layer to pre-1980 levels is expected by the mid 21st century [14].

UV-B radiation is potentially damaging to plants, impairing gene transcription and translation, as well as photosynthesis [15]. The biological impact of UV-B radiation depends on a number of factors, including the ratio of UV-B to PAR, the spectral distribution within the UV-B wavelength band, genetic factors and the exposure-history of the plant [15,16]. As a result, it is often difficult to compare different UV-exposure studies. Notwithstanding this difficulty, there is overwhelming evidence that UV-B radiation induces complex changes in gene expression, as well as DNA repair capacity, photosynthetic activity, plant morphology, and pest-, and pathogen-resistance. These aspects of UV-biology have been extensively reviewed [15,16]. Furthermore, various studies have explored whether UV-B acclimation responses can be exploited to manipulate plant architecture [17] or disease resistance [18], in a commercial context. Glasshouses and polytunnels are mostly UV-B-free. The development, however, of different types of glass or plastic facilitates selective penetration of some, or all, UV-wavelengths into glasshouses or polytunnels [19]. Alternatively, UV-supplementation setups, based on UV-

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