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Review

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

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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.

Contents

1. Life is stressful for a plant . . . 450
2. Plant stress responses and nutritional value . . . 450
3. UV-B radiation as an environmental stressor . . . 450
4. UV-B-induced changes in accumulation of antioxidants and secondary metabolites . . . 451
   4.1. UV-impacts on ascorbate, glutathione and tocopherol metabolism . . . 452
   4.2. Polyamines . . . 452
   4.3. Plant phenolics . . . 453
   4.4. Alkaloids . . . 454
   4.5. Phytosterols . . . 455
   4.6. Cyanogenic glycosides and glucosinolates . . . 455
   4.7. Isoprenoids . . . 455
5. Do UV-B-induced changes in the plant secondary metabolite pool affect human consumers? . . . 456
   5.1. UV-induced changes in the plant metabolome are complex . . . 456
   5.2. UV-induced changes in the plant metabolome versus nutritional and/or pharmaceutical value . . . 456
6. Conclusion . . . 457
   Acknowledgements . . . 457
   References . . . 457

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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.

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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-

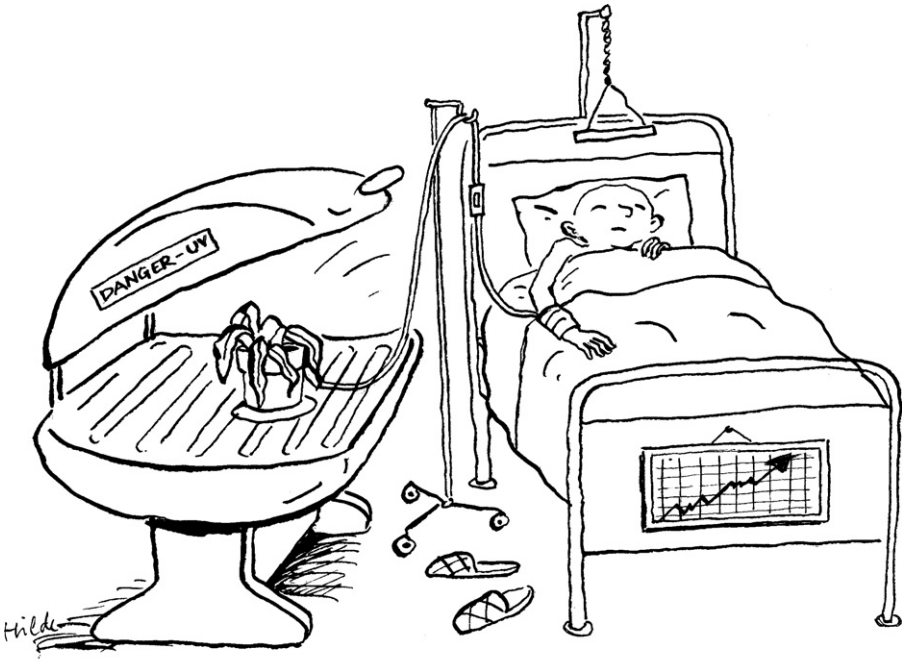

Fig. 1. The UV-B-induced accumulation of flavonoids and tocopherols, metabolites with documented health benefits, triggers the question whether or not UV-acclimated crops have nutritional and/or pharmaceutical benefits for human consumers.

emitting fluorescent tubes, can be used to obtain higher than ambient levels of UV-B radiation. Ultraviolet supplementation has been proposed as a cultivation measure to increase levels of tocopherol [20] and flavonoid [21] in vegetable crops. Both metabolites have desirable nutritional and pharmacological characteristics. This triggers the question whether or not UV-acclimated crops have additional nutritional and/or pharmaceutical benefits for human consumers (Fig. 1). Our analysis of the literature highlights the complexities of UV-B-induced metabolic acclimation responses, in terms of dose–response curves and induction kinetics as well as the large range of metabolites that is involved. The full complexity of the UV-B-induced metabolic response has not yet been reported in the literature. We will show the inadequacies of current studies of UV-B-induced metabolic responses and conclude that only large meta-studies can fully gauge the effects of UV-B radiation on plant metabolic composition, and appraise potential effects of UV-B irradiation on the nutritional or pharmacological quality of plant based human foods.

4. UV-B-induced changes in accumulation of antioxidants and secondary metabolites

Our understanding of UV-B-induced changes in metabolite levels is largely centred on the UV-screening flavonoids [15,16]. The focus on accumulation of these phenolic compounds has, perhaps, obscured the fact that UV-B induces changes in a range of

Table 1
Effects of UV-B exposure on antioxidants

UV-B treatment	Plant material	Biological impact	Reference
Acute exposure (30–120 min) to 0.46 kJ m^{-2} min^{-1} UV-B	Broad bean (*Vicia faba*) detached leaves	4-fold increase in DHA level	[22]
Acute exposure to a dose-rate of 1.4 W m^{-2} supplemental UV-$B_{be,300}$	Pea (*Pisum sativum*) plants	4.0- and 1.4-fold increase in total GSH level after 48 or 144 h UV-exposure, respectively 60-fold increase in GSSG levels after 48 h UV	[23]
Acute exposure (50 or 100 min) to a dose-rate of 5.2 W m^{-2} supplemental UV-$B_{be,300}$	Sunflower (*Helianthus annuus*) cotyledons	1.5-fold (50 min) and 1.4-fold (100 min) increase in Asc level 1.5-fold (50 min) and 1.4-fold (100 min) increase in DHA level 13-fold (50 min) and 6-fold (100 min) increase in GSH level 5-fold (50 min) and 3-fold (100 min) increase in GSSG level	[24]
Two weeks growth under low, supplemental UV-B (4, 8 or 24 h day^{-1}) giving doses of 1, 2 or 6 kJ m^{-2} day^{-1} UV-B_{be}	Spinach (*Spinacea oleracea*) plants	2.7-, 1.9- and 0.9-fold increase in Asc level, after 4, 8 and 24 h UV-B, respectively	[25]
Acute exposure (90–180 min) to 2.7 or 5.4 kJ m^{-2} day^{-1} UV-B_{be}	Spinach (*Spinacea oleracea*) thylakoids	30% decrease in α-tocopherol levels	[26]
Exposure for up to 5 days to supplemental 8.35 kJ m^{-2} day^{-1} UV-B_{be}	Maize (*Zea mays*) plants	15%, 19% and 5% decrease in α-tocopherol levels after 1, 2 and 3 days UV-B exposure, respectively	[27]
Exposure for 3 days to a dose-rate of 26 W m^{-2}	Cucumber (*Cucumis sativus*) cotyledons	50% decrease in α-tocopherol level 30% increase in Asc level	[28]
Exposure for 1 week to a dose-rate of 21–35 W m^{-2}	Lettuce and spinach plants	8.2- and 7.8-fold increase in α-tocopherol level in lettuce and spinach, respectively	[20]

different plant metabolites, including anti-oxidants, alkaloids and isoprenoids.

4.1. UV-impacts on ascorbate, glutathione and tocopherol metabolism

Ascorbate and glutathione are ubiquitous components of the anti-oxidative stress defence and signalling system of plants [2]. Ascorbate also acts as an anti-oxidant in humans and is an essential component of the human diet. Plants are the main source of ascorbate (vitamin C) for humans. Substantial variations occur in ascorbate levels and oxidation state depending on whether plants were subjected to acute, severe UV-B stress or mild, chronic UV-B stress (Table 1). Exposure to acute UV-B stress results in net oxidation of ascorbate and the accumulation of monodehydroascorbate [22]. In contrast, under chronic UV-exposure conditions the ascorbate pool increases, which reflects the stress acclimation process [25]. We interpret these two scenarios as the extremes of a response continuum that is characterised by varying contributions of the stress and acclimation components on ascorbate and/or glutathione metabolism. Under intermediate UV-exposure conditions both components are present. For example, acclimation of plants under a relatively high, acute UV-B dose resulted in an increase in total glutathione, as well as a simultaneous increase in the oxidation states of the pool [23]. Thus far, the full dose–response curves of ascorbate and glutathione metabolism in response to UV-B exposure have not been determined, hampering attempts to assess the impact of realistic UV-B levels on crop nutritional value.

Tocopherols are lipid-soluble plant antioxidants. These compounds are precursors of vitamin E, which humans take up with plant-derived oils and fats. Vitamin E deficiency in humans is mostly linked with neurological disorders. In plants, tocopherols are implicated in the reduction of polyunsaturated fatty acid radicals that are formed in UV-B stressed plants [26]. Short-term, acute UV-B exposure triggers a decrease in α-tocopherol levels in plants [26–28], possibly reflecting reactions with lipid radicals. The UV-B induced decrease in α-tocopherol levels has been reported to be paralleled by an increase in ascorbate levels [28]. Previously, analysis of *Arabidopsis* single or double mutant plants had shown that decreases in the levels of one of the three main plant oxidants, tocopherols, ascorbate or glutathione, resulted in increases in the remaining antioxidants [29]. We hypothesise that similar compensatory interactions between pools of water and lipid-soluble antioxidants occur in plants that are being acclimated to UV-B radiation. Long-term UV-acclimation can, however, result in increases in ascorbate and tocopherol levels [20], an observation that is important from a nutraceutical perspective. Interestingly, the expression of tocopherol biosynthesis genes is upregulated in *Arabidopsis* plants exposed to an acute UV-dose, but remains unchanged in plants raised under chronic UV-B [30,32]. The lack of increased tocopherol biosynthetic capacity under chronic UV-conditions, suggests that the enhanced tocopherol levels in UV-B acclimated plants are the result of an overreaction by the plant, possibly to oxidative stress during initial UV-B exposure. A remarkably similar kinetic can be observed in the expression of the pyridoxine (vitamin B6) biosynthesis gene *PyroA*. *PyroA* expression increases following exposure to acute stress, and this has been associated with the singlet oxygen scavenging properties of pyridoxine [31]. *PyroA* expression is downregulated in plants acclimated to low chronic UV-B [32]. These data imply that increased UV-B tolerance in UV-acclimated plants is not primarily via enhanced anti-oxidative defences.

4.2. Polyamines

Polyamines are small, aliphatic amines that are associated with regulation of photosynthesis, developmental processes, and in particular cell growth and division in plants. Plants accumulate polyamines when exposed to abiotic or biotic stresses, possibly to control expression of stress protection pathways [33]. Yet, there appears to be no consensus with respect to the effects of UV-B radiation on plant polyamine levels (Table 2). Chronic treatment of plants with low UV-B doses resulted in either increases or decreases in polyamine levels (Table 2). Decreases in free polyamines appear to be linked to severe stress, and growth retardation, whilst increases appear to be transient peaking after 3 days of UV-B exposure [34]. Indeed, at least two-polyamine biosynthesis-related genes are upregulated in *Arabidopsis* following short-term UV-exposure, although several polyamine-biosynthesis genes are downregulated following acclimation to chronic low UV-B [30,32]. The transient increase in thylakoid associated polyamine levels has been speculated to contribute to UV-protection, prior to the accumulation of, among others, carotenoids and flavonoids [34]. Given this complex relation between plant stress acclimation and polyamine levels, it is not surprising that polyamine levels in food products have been

Table 2
Effects of UV-B radiation on polyamine levels

UV-B treatment	Plant material	Biological impact	Reference
Exposure for up to 7 days to a dose-rate of 1 W m^{-2} supplemental UV-B	Tobacco (*Nicotiana tabacum*) Bel B plants	8- and 3-fold increase in chloroplast associated spermidine and putrescine levels, respectively, after 7 days of UV-B 4.5- and 8-fold increase in thylakoid associated spermidine and putrescine levels, respectively, peaking after 3 days of UV-B exposure, and decreasing subsequently	[34]
Exposure for up to 7 days to a dose-rate of 1 W m^{-2} supplemental UV-B	Tobacco (*Nicotiana tabacum*) Bel W3 plants	8- and 5-fold increase in chloroplast associated spermidine and putrescine levels, respectively, after 7 days of UV-B 80% decrease in both thylakoid associated spermidine and putrescine levels after 3 days of UV-B, recovery to control values by day 7 Changes in polyamines paralleled by stress symptoms, including decreases in chlorophyll and carotenoid levels	[34]
Exposure for up to 14 days to supplemental doses of 5.3 or 10.7 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$	Bean (*Phaseolus vulgaris*) plantlets	20% decrease in spermine levels after 14 days UV-B 20% and 50% decrease in putrescine levels at days 6 and 14, respectively 45% decrease in overall polyamine levels Plant stress indicated by decrease of plant growth rate	[35]
Exposure for up to 18 days to supplemental doses of 8.8 or 12.6 kJ m^{-2} UV-B	Cucumber (*Cucumis sativus*) plantlets	100%, 50% and 250% increase in putrescine, spermidine, and spermine levels, respectively, after 12 days of UV-exposure Minor decrease in polyamine levels on day 18, associated with stress symptoms	[36]

Table 3
Effects of UV-B exposure on flavonoids

UV-B treatment	Plant material	Biological impact	Reference
Exposure for 10 days to supplemental doses of 3.6 (ambient) kJ m^{-2} day^{-1} or 7.18 (enhanced) kJ m^{-2} day^{-1} UV-B_{be}	Willow (*Salix myrsinifolia*) cloned plants	1.1- to 1.3-fold increase in levels of luteolin derivatives under enhanced UV 1.3- to 1.8-fold increase in levels of myricetin derivatives under enhanced UV No change in level apigenin derivatives	[39]
Exposure for 4 weeks to supplemental doses of 3.6 (ambient)kJ m^{-2} day^{-1} or 7.2 (enhanced)kJ m^{-2} day^{-1} UV-B_{be}	Willow (*Salix myrsinifolia* × *Salix myrsinites*) plants	1.5-fold increase in levels apigenin derivatives under enhanced UV 3-fold increase in levels luteolin derivatives under enhanced UV	[40]
Exposure for 7 days to a supplemental dose of 13 kJ m^{-2} day^{-1} UV-B_{be}	Barley (*Hordeum vulgare*) seedlings	1.3-fold increase in saponarin level under UV 5.1-fold increase in lutonarin level under UV	[41]
Exposure for 58 or 76 days to supplemental doses of 1–1.3 (ambient) kJ m^{-2} day^{-1} or 6.7–7.2 (enhanced) kJ m^{-2} day^{-1} UV-B_{be}	Birch (*Betula pendula*) seedlings	1.47-fold increase in levels quercetin derivatives under enhanced UV 1.36-fold increase in levels myricetin derivatives under enhanced UV	[42]
Exposure for up to 21 days to a supplemental dose of 4.8 kJ m^{-2} day^{-1} UV-B_{be}	Scots pine (*Pinus sylvestris*) seedlings	Up to 2.2-fold increase in levels quercetin derivatives under UV Up to 2-fold increase in kaempferol (astragalin) level under UV	[43]
Exposure for up to 6 weeks to supplemental doses of 0 (mylar foil), 0.8–4.5 (ambient)kJ m^{-2} day^{-1} or 2.8–6.8 (enhanced)kJ m^{-2} day^{-1} UV-B_{be}	Buckwheat (*Fagopyrum esculentum*) plants	Rutin content ranged between 1.4, 2.8 and 1.9% of dry weight, for no-UV-B, ambient UV-B and enhanced UV-B, respectively	[44]
Exposure for 48 h to a dose-rate of ca. 1.12 W m^{-2} of solar UV-B	White mustard (*Sinapis alba*) plants	7-fold increase in quercetin derivatives under UV 2-fold decrease in kaempferol derivatives under enhanced UV	[45]

identified as 'variable' [37]. Dietary polyamines control human cell growth and proliferation, and their role in controlling tumour growth is being studied [37]. Consequently, a better understanding of the role of environmental stress in controlling accumulation of these compounds in the plant is desirable [37].

4.3. Plant phenolics

The accumulation of plant phenolics, including hydroxycinnamic acids, flavonoids, and complex polymeric lignin or tannin-like compounds has been studied in numerous plant species, exposed to a range of different stress conditions [38]. Many phenylpropanoid derivatives selectively absorb in the UV-B region of the spectrum, while not decreasing penetration of photosynthetic radiation into the leaf. This characteristic, together with their antioxidant activity, makes plant phenolics ideally suited for a role in UV-protection [38].

Flavonoids are accumulated by a broad range of plants following UV-exposure (Table 3). This response is often visualised as an increase in UV-absorbance of methanolic extracts. However, such analysis of "overall" UV-B absorbance does not reveal that different flavonoid derivatives accumulate in different species and/or under different environmental conditions (Table 3). Moreover, the limited dose–response data that are available, indicate a complex relation between UV-exposure and the accumulation of specific flavonoid species. For example, rutin, a glycosylated quercetin derivative that is the main UV-B-induced flavonoid in buckwheat (*Fagopyrum esculentum*), was present at low levels in control plants that were raised without UV-B, high levels in plants raised under moderate UV-B, and low levels again in plants raised under a high UV-B dose [44]. It remains to be elucidated how (and whether) this "optimum" dose–response relates to other metabolic changes, including decreases and increases in ascorbate, glutathione and tocopherol under acute and chronic stress, respectively (Table 1). The lack of rutin accumulation under high UV-B may reflect damage and an inability to sustain rutin synthesis under high UV-B levels. However, it is also possible that this comprises part of a physiological acclimation response that involves the accumulation of different protectants under different UV-levels. There is some experimental support for the latter scenario. The relative abundance of different flavonoid species changes following UV-exposure, which implies that the dose–response curves for the accumulation of individual flavonoid-compounds differ. For example, the ratio of quercetin to kaempferol increases in many UV-B exposed plants [45]. Quercetin and kaempferol have similar extinction coefficients in the UV-region of the spectrum. Yet, quercetin is a more efficient ROS-scavenger than kaempferol, due to its higher number of hydroxyl groups. It is this type of enhanced antioxidant property of flavonoids which have often been associated with "nutritional benefits". Yet, doubts have arisen on the importance of the antioxidative capacities of plant phenolics in determining the health benefits for human consumers [46,47]. During the course of absorption into the human body, flavonoids are extensively modified by methylation, sulphation or glucuronidation of hydroxyl-groups [46]. Such modifications will decrease antioxidant activity and nullify the significance of increased quercetin to kaempferol ratios in plant-based foods. Instead, there is now increasing evidence that the health benefits of dietary plant polyphenols, once taken up in human plasma, relate to interactions of heavily modified phenolic structures with a range of protein targets including oxygenases, telomerases and receptors like the human oestrogen receptor [47]. The uptake of plant polyphenols in to human plasma is, however, both limited [46] as well as variable, depending on the specific metabolite [47]. Indeed, the chemical structure of the polyphenols, rather than the concentration, determines the rate and extent of absorption in the human plasma [47], and this implies that UV-B induced increases in overall flavonoid levels cannot simply be equated with nutritional benefits.

Table 4
Effects of UV-B exposure on phenolic acids

UV-B treatment	Plant material	Biological impact	Reference
Exposure for 10 days to supplemental doses of 3.6 (ambient)kJ m^{-2} day^{-1} or 7.18 (enhanced)kJ m^{-2} day^{-1} UV-B_{be}	Willow (*Salix myrsinifolia*) cloned plants	Up to 15% increase in levels of hydroxycinnamic acid derivatives under enhanced UV Up to 20% decrease in salicin level under enhanced UV	[39]
Exposure for 4 weeks to supplemental doses of 3.6 (ambient)kJ m^{-2} day^{-1} or 7.2 (enhanced)kJ m^{-2} day^{-1} UV-B_{be}	Willow (*Salix myrsinifolia* × *Salix myrsinites*) plants	Up to 80% increase in chlorogenic acid level under enhanced UV Up to 80% increase in levels of cinnamic acid derivatives under enhanced UV Up to 10% increase in total salicylate level under enhanced UV	[40]
Exposure for 48 h to a dose-rate of ca. 1.12 W m^{-2} of solar UV-B	White mustard (*Sinapis alba*) plants	No change in levels of hydroxycinnamic acids	[45]
Exposure for up to 30 days to supplemental doses of 8.8 or 13.6 kJ m^{-2} day^{-1} UV-B_{be}	Barley (*Hordeum vulgare*) plants	Level of soluble ferulic acid unchanged on days 5 and 20 Level of soluble ferulic acid increased on days 10 and 15	[49]
Exposure for 18 days to a supplemental dose of 2 kJ m^{-2} day^{-1} UV-B_{be})	Sweet basil (*Ocimum basilicum*) plantlets	44% decrease in methyleugenol level under UV 69% increase in eugenol level under UV	[50]
Exposure for 2 weeks to supplemental doses of 5.4 or 31 kJ m^{-2} day^{-1} UV-B_{be}	Rosemary (*Rosmarinus officinalis*) plants	4- and 287-fold increase in caffeic acid level under low and high UV-B dose, respectively 1.1- and 2.3-fold increase in rosmarinic acid level under low and high UV-B dose, respectively 2.3 and 1.3-fold increase in vanillic acid level under low and high UV-B dose, respectively	[52]
Exposure for 58 or 76 days to supplemental doses of 1–1.3 or 6.7–7.2 kJ m^{-2} day^{-1} UV-B_{be}	Birch (*Betula pendula*) seedlings	1.4-fold increase in chlorogenic acid level at both time points	[42]

The contribution of mono- or bi-phenolic acids to the UV-screening capability of plants is less well understood than that of flavonoid compounds. Phenolic acids are UV-absorbing pigments, yet these compounds do not necessarily accumulate in UV-B exposed plants (Table 4). Lack of phenolic acid accumulation may reflect the distribution of (limiting) substrates among the different branches of the phenylpropanoid network, a phenomenon that is, for example, visualised as a change in the sinapate ester to flavonoid ratio in *Arabidopsis tt4*-mutants with impaired chalcone synthase activity [48]. Indeed, while many studies have reported UV-B induced increases in flavonoids, the effects on phenolic acid levels are more variable (Table 4). Levels of the pharmacologically active compounds salicin (chemically similar to acetylsalicylic acid (aspirin)) in willow (*Salix myrsinifolia*) and methyleugenol in basil (*Ocimum basilicum*), decreased in plants exposed to long-term UV-B [39,50]. The presence of methyleugenol in foodstuffs is of nutritional concern because of its carcinogenic and teratogenic properties. Currently much of the basil that is grown for human consumption (oil and/or pesto) is raised in the absence of UV-B, in glasshouses, where methyleugenol accumulation can be significant [50]. In contrast, levels of caffeic, rosmarinic [52] and chlorogenic acid [40] have all been reported to increase upon exposure to UV-B. Rosmarinic acid is a strong anti-oxidant that has anti-inflammatory properties in humans, while caffeic acid has anti-carcinogenic properties [51]. Superficially, these data indicate that UV-B exposure may improve the nutritional quality of basil or rosemary, by decreasing accumulation of a toxic compound (i.e. methyleugenol) or increasing accumulation of compounds with proven health benefits (rosmarinic acid and caffeic acid). Yet, in the absence of data on the dose–response relationships for the accumulation of different phenolic acids, any suggestion about improved nutritional quality is premature. Indeed, in barley (*Hordeum vulgare*) leaves the levels of soluble ferulic acid transiently increased following UV-B exposure, but returned to pre-exposure levels after some 20 days of UV-B exposure [49]. The conclusion based on such data is that single time-point analysis of an acclimation process does not necessarily reveal the extent of a dynamic biological stress response.

4.4. Alkaloids

The alkaloids constitute a family of secondary metabolites, many of which have been identified as plant defence compounds, toxins or medicines. One of the most extensively studied alkaloids is nicotine. Production of this UV-absorbing compound increased in tobacco callus exposed to UV-B [57], although this has not been confirmed by studies on whole plants. UV-B radiation does, however, induce accumulation of two quite distinct alkaloids, nicotinamide, and the derived metabolite trigonelline, in plants [23]. Accumulation of these compounds is associated with severe stress, including DNA-strand breakage. Nicotinamide and trigonelline levels remain unchanged in plants exposed to low doses of UV-B [23]. Clearly, the induction profile of these two compounds is distinct from that of a range of other metabolites, including ascorbate, glutathione and polyamines, that accumulate under low, chronic UV-B doses, but less so under damaging UV-B levels (Table 1). This suggests that distinct regulatory pathways control accumulation of different metabolites. One other alkaloid that is reported to accumulate in plants exposed to supplemental UV-B is brachycerine, an indole alkaloid produced in *Psychotria brachyceras* [58]. It has been proposed that the accumulation of brachycerine is related to its antioxidative and UV-absorbing activities [58]. The alkaloids from *P. brachyceras* are pharmacologically of interest, as they have been associated with analgesic activity.

Tens of thousands of alkaloids have been identified in plants. Yet, it is remarkable that there are so few reports on the UV-B mediated accumulation of these compounds. Micro-array analysis of UV-B acclimated *Arabidopsis* revealed downregulation of strictosidine biosynthesis genes [32], although we are not aware of reports on UV-induced changes in the levels of this indole alkaloid. Perhaps, expression of strictosidine biosynthesis genes is not limiting for strictosidine accumulation. However, we consider

Table 5
Studies on the effects of UV-B radiation on isoprenoids

UV-B treatment	Plant material	Biological impact	Reference
Exposure for up to 3 days to dose of 8.35 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$	Maize (*Zea mays*) seedlings	1.25- and 1.05-fold decrease in zeaxanthin levels under UV-B, on days 1 and 3, respectively 1.19- and 1.02-fold decrease in β-carotene level under UV-B, on days 1 and 3, respectively	[62]
Long-term growth under ambient, solar UV-B or under reduced UV-B (blocking filters)	Vine (*Vitis vinifera*) plants	2.5-fold increase in lutein level under UV in grapes, irrespective of developmental stage 1.6-fold decrease in β-carotene level in young (green) grapes under UV-B 2.45-fold increase in β-carotene level in mature (blue) grapes under UV-B	[63]
Long-term growth under ambient, solar UV-B or under reduced UV-B (blocking filters)	Grass (*Deschampsia antarctica*) plants	No UV-B effect on lutein, neoxanthin, violaxanthin or β-carotene levels	[64]
Two weeks growth under supplemental dose of 13 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$	Rapeseed (*Brassica napus*) plants	No UV-B effect on violaxanthin, antheraxanthin, zaxanthin or β-carotene levels	[65]
Two weeks growth under supplemental UV-B	Basil (*Ocimum basilicum*) plantlets	2.7-, 2.4- and 2.6-fold increases in pinene, cineole and linalool levels, respectively, under UV-B. Increases are do occur in established, but not in young, seedlings	[66]
Growth for 12 weeks under solar UV-B (ca. 7.5 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$), or solar UV-B plus added dose of 4.5 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$	Yarrow (*Achillea millefolum*) plants	8-fold decrease in the level of the volatile terpene, E-B-santolina-epoxide, under enhanced UV No UV-significant effect on 11 further, volatile isoprenoids	[67]
Two weeks growth under supplemental doses of 5.4 or 31 kJ m^{-2} day^{-1} $UV\text{-}B_{be}$	Rosemary (*Rosmarinus officinalis*) plants	1.5- and 1.8-fold increase in carnosic acid under low or high UV, respectively	[52]
Exposure for 3 days to supplemental dose-rates of 1.13 W m^{-2}, or 15 days 0.43 W m^{-2}	Liquorice (*Glycyrrhiza uralensis*) plants	1.3- and 1.4-fold increase in glycyrrhizin in the roots after short, or long-term UV-exposure, respectively	[68]

it more likely that strictosidine levels have not been assayed in UV-B acclimated plants and that the same argument also applies to many other alkaloids.

4.5. Phytosterols

Phytosterols limit absorption of cholesterol from fat matrices into the human intestinal tract, which results in lower cholesterol levels in consumers and decreases the incidence of cardiovascular disease [12]. This property makes phytosterols valuable nutraceuticals that are used to fortify a range of food products. In plants, expression of two steroid biosynthesis genes is increased under chronic UV-B, and this has been related to regulation of brassinosteroid biosynthesis [32]. The phytosterol ergosterol can also be converted into plant vitamin D2 (ergocalciferol), a reaction that is known to be catalysed by UV-B radiation. Yet, we are not aware of UV-B-induced changes in either phytosterol or vitamin D2 metabolite levels in plants raised under realistic UV-B doses.

4.6. Cyanogenic glycosides and glucosinolates

Cyanogenic glycosides are toxins associated with biotic-stress defence. UV-B acclimation of white clover (*Trifolium repens*) resulted in an increase in the capability to produce cyanide [59]. This observation contributes to the concept of crosstalk between pest and disease resistance pathways and UV-acclimation that has been identified in several studies [18]. Another class of toxic defence compounds are the glucosinolates. These isothiocyanate glycosides are present in members of the Brassicaceae family and are studied because of their anti-carcinogenic activities. Exposure to natural UV-B doses decreased levels of specific glucosinolates in several plant species [45]. Consistently, four glucosinolate biosynthesis genes were downregulated in *Arabidopsis* grown under chronic UV-B [32]. Intriguingly, in short-term experiments UV-B has been reported to activate both the jasmonic acid and salicylic acid pathways, which are associated with enhanced glucosinolate synthesis. Yet, long-term UV-experiments show UV-B induced decreases in both cyanogenic glycosides and glucosinolates. We interpret this paradox as yet another example of the distinct characters of acute and chronic stress responses.

4.7. Isoprenoids

Isoprenoids regulate growth, biotic stress tolerance, pigmentation and photosynthesis. The tetraterpenoid β-carotene is also an essential component of the human diet. This metabolite is a precursor for vitamin A and protects against several diseases and night blindness. In plants, carotenoids are antioxidants that are associated with scavenging of singlet oxygen in the chloroplast. Exposure to acute UV-B results in decreases in levels of xanthophylls as well as carotenes [62], indicating oxidative stress. Gene-expression analysis revealed that several carotenoid biosynthesis genes are upregulated following exposure to acute UV-B [30], but downregulated following exposure to chronic UV-B [32]. We interpret these data as reflecting the production of carotenoids as a rapid response to UV-B. Most long-term UV-exposure studies show no, or only small changes, in carotenoid levels (Table 5). This indicates a lack of oxidative stress in well-acclimated plants and implies that acclimated plants are protected through other means, including, most likely, UV-screening pigments.

Glycyrrhizin is a bioactive glycosidic triterpenoid that is accumulated by *Glycyrrhiza uralensis* (liquorice). This compound is a natural sweetener with potential anti-tumor and anti-viral activities [68]. UV-B exposure studies revealed an optimum UV-dose for glycyrrhizin accumulation, with exposure to high UV-doses resulting in decreased glycyrrhizin accumulation [68]. A similar type of dose–response has also been observed for the flavonoid, rutin [44], indicating commonalities in the induction kinetics of metabolically distinct classes of compounds. Remarkably, UV-induced glycyrrhizin accumulates in roots, which were

not directly exposed to UV-B radiation. This shows that UV-B-induced changes in metabolite accumulation are systemic, and not limited to tissues directly exposed to the stress.

The mono- and diterpenes include many aromatic substances and essential oils. Carnosic acid is a powerful lipophilic ROS-scavenger present in rosemary (*Rosmarinus officinalis*) oil extracts which is used as food additive, proposed as human dietary factors and investigated as inhibitor of skin tumorgenesis [52]. Carnosic acid levels doubled in leaves of rosemary exposed to chronic UV-B [52], a finding that has pharmaceutical relevance. Supplemental UV-B also stimulated accumulation of volatile monoterpenes in some species [66,67]. In basil, accumulation of terpenoid compounds only occurred once seedlings had reached a specific developmental stage [66]. These data mirror the observation that the UV-B-induced accumulation of β-carotene only occurs in grapes that are beyond a specific developmental stage [63]. The possibility that UV-B-induced metabolic responses are co-controlled by developmental parameters is rarely considered, and might explain some of the discrepancies that are present in the literature.

5. Do UV-B-induced changes in the plant secondary metabolite pool affect human consumers?

Many UV-B studies comprise measurements of a single class of metabolites at a single time-point, following exposure of a single plant species to a single UV-B dose-rate. Despite the obvious limitations of data acquired in such studies, we were able to discern tantalising glimpses of complex UV-acclimation kinetics. The complexity of these UV-B-induced acclimation responses has, thus far, not been recognised.

5.1. UV-induced changes in the plant metabolome are complex

Stress-induced changes in metabolic profiles depend on the specific plant species and/or cultivar, its developmental state, the severity and the dynamics of stress exposure, and other environmental parameters, and involve all major groups of secondary plants metabolites. Much work is needed to detail the responses of specific plant metabolites to UV-B radiation. However, it is clear that dose–response relationships vary for different (classes of) metabolites. Our survey of the literature recognises five, not mutually exclusive, groups of metabolites, depending on their induction by UV-B radiation.

1. Metabolites whose levels increase with increasing UV-B dose (e.g. flavonoids).
2. Metabolites whose levels are associated with severe UV-B-induced stress (e.g. nicotinamide and trigonelline [23]).
3. Metabolites that accumulate transiently during the UV-B acclimation process (e.g. polyamines [34] and ferulic acid [49]).
4. Metabolites, with anti-oxidative properties, and whose levels decrease to varying extents under short-term, acute UV-B exposure but increase when plants are acclimated to long-term UV-B (e.g. ascorbate, glutathione, tocopherol (Table 1) and carotenoids (Table 5)).
5. Metabolites whose levels peak under moderate UV-B doses, and are considerably lower under both low and high UV-B doses (e.g. rutin [44] and glycyrrhizin [68]).

It has been speculated that the complexity of UV-B-induced metabolic changes reflects balancing of fast, short-term responses with slower, long-term responses, as visualised by the accumulation of polyamines and flavonoids [34]. We hypothesise that plants when initially exposed to acute UV-B radiation will experience oxidative stress, as indicated by decreases in ascorbate, glutathione, tocopherol and carotenoid levels (Fig. 2 and Tables 1 and 5). Acclimation will comprise of increases in total anti-oxidant activity, increases that will be made gradually superfluous when levels of UV-screening pigments have sufficiently increased to limit the penetration of UV-B radiation into the plant tissues (Fig. 2). This triggers interesting questions concerning the regulatory mechanisms coordinating the induction of different metabolites. The currently most common type of UV-B exposure study (2 doses of the stressor & 1 time point) is inadequate to comprehensively reveal stress-induced changes in the plant metabolome and/or to test models of coordinated metabolite induction (Fig. 2). We conclude that only large meta-studies can fully gauge the effects of UV-B radiation on plant metabolic composition. Such studies need to consider time-, and dose-dependency, severity of the imposed stress, and a broad range of relevant metabolites. The development of metabolomic techniques during the last decade enables this type of study.

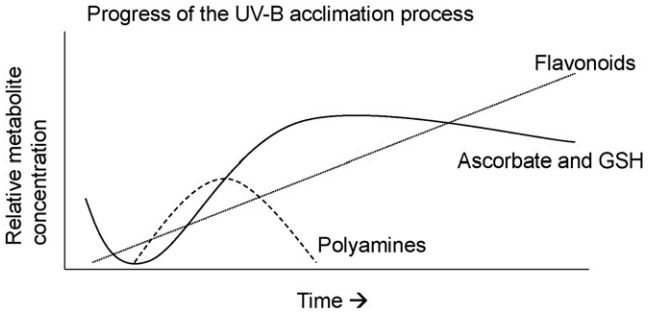

Fig. 2. Schematic model showing the changes in metabolite levels that occur in plants during the UV-B acclimation process. Levels of ascorbate and glutathione initially decrease during exposure to acute UV-B stress, with the extent of this decrease depending on the severity of the imposed oxidative stress (Table 1). Following an initial decrease, antioxidant levels increase in plants acclimated to chronic UV-B conditions. Polyamines transiently accumulate during early stages of the acclimation process (Table 2), whilst levels of flavonoids increase gradually during UV-B acclimation (Table 3).

5.2. UV-induced changes in the plant metabolome versus nutritional and/or pharmaceutical value

Many abiotic and biotic stress conditions induce complex metabolic acclimation responses. Cultivation strategies also impact on secondary metabolite accumulation in plants and this is reflected in the differences between organic and conventionally produced crops [69]. The accurate determination of acclimation-associated changes in the plant metabolome is directly relevant in the context of (1) food nutritional value, (2) safety of multi-component herbal extracts, and (3) extractable content of specific active molecular compounds.

Our review of the literature has revealed UV-B-induced changes in the levels of various metabolites with nutritional and/or pharmaceutical value. Yet, the assessment of the pharmacological and/or nutritional value of such changes within a poorly documented mixture of plant metabolites is complicated [70]. In a mixture, metabolites may have potentiating, antagonising and/or synergistic effects [71]. Moreover, dietary benefits may arise from a broad range of additional plant-derived factors, including the presence of dietary fibres, mono-unsaturated fatty acids, immuno-stimulatory agents, minerals and ethanol [46]. These factors can impact on interactions of metabolites with specific molecular targets, or rather affect digestibility and/or uptake of plant material. Indeed, the bioaccessibility of β-carotene ranges from 47% in kiwi fruits to 30% in spinach and just 2% in red grapefruits,

whilst the bioaccessibility of lutein is 100%, 19% and 100% for the same food products, respectively [60]. Indeed, bioaccessibility of carotenoids varies depending on the crop species, the particular carotenoid and its isomeric form [61].

Two determinants of general metabolite bioavailability are tannin and lignin concentrations. Tannins have anti-feeding effects, due to their protein binding properties, whilst lignin decreases digestibility of plant material. Levels of condensed tannins were found to increase with UV-B exposure in some species [53,54], but decrease in others [39]. Similarly, lignin levels were found to increase in some UV-B exposed plants [56], while decreasing in others [55]. Therefore, the validity of any conclusion on potential nutritional and/or pharmaceutical benefits of plant material, based on measurements of a single (class of) metabolite must be questioned. Conversely, the reproducibility of multi-component plant-based drugs will be limited, unless plants are raised under carefully controlled conditions [71]. "Botanical drugs" are multi-component plant mixtures that have undergone rigorous testing, and in which levels of the active ingredient (but not necessarily that of other metabolites) have been standardised [71]. In contrast, dietary supplements and nutraceuticals, are not subject to the same level of rigorous testing as drugs. Our analysis reveals complex effects of UV-exposure on the composition of the plant metabolome. Therefore, it is likely that stress-exposure will cause a degree of unpredictability with respect to the nutritional or pharmaceutical effectiveness of dietary supplements and/or nutraceuticals. Claims that plants raised under specific cultivation conditions, including supplemental UV-B, convey nutritional and/or pharmaceutical benefits (Fig. 1) must be treated with some scepticism, if only because of the complexity of the stress-induced metabolic responses. On the other hand, stress-acclimation can be exploited to improve yields of single-component drugs that are extracted from plants, i.e. plants as biochemical factories. Our survey of the literature indicates that targeted induction of specific metabolites is a precision process that requires detailed understanding of the dynamics and temporal character of plant stress responses.

6. Conclusion

Our survey of stress-induced changes in plant metabolite levels emphasises the complexity of plant responses. Responses are species and/or cultivar specific, and depend on the severity and the dynamics of stress exposure, as well as other environmental parameters. Any increase in the accumulation of a nutritionally "desirable" plant metabolite should be viewed in the context of a complex, overall change in the metabolic profile in which levels of many different compounds change in parallel. This emphasises the importance of determining in full, the stress-induced changes in the plant metabolome, in order to assess nutritional and/or medicinal consequences of plant stress acclimation.

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