

ULTRAVIOLET-B RADIATION : A POTENT ELICITOR OF PHENYLPROPANOID PATHWAY COMPOUNDS

Swabha Takshak* and Shashi Bhushan Agrawal**

Laboratory of Air Pollution and Global Climate Change, Department of Botany,
Institute of Science, Banaras Hindu University, Varanasi-221005, India
*e-mail: swabha.1987@gmail.com **e-mail: sbagrwal56@gmail.com

Abstract

Although no longer considered a stress factor due to the successful implementation of Montreal Protocol in 1987 and consequent reductions in ozone depleting substances, ultraviolet (UV)-B radiation (a direct consequence of stratospheric ozone depletion) levels are far from reaching their pre-1980 status. Plants have developed various protective measures to counteract the adverse effects of this stress factor. One of the important defence strategies of plants against UV-B radiation is the biosynthesis of enhanced concentrations of secondary metabolites. For the biosynthesis of these metabolites, the phenylpropanoid pathway is ubiquitous in plants. This pathway leads to the biosynthesis of various phenolic compounds many of which play an important role not only in plant adaptation and survival, but also in various aspects pertaining to human health and nutrition. This review presents an overview of the current UV-B scenario, its effects on plants, and the defence strategies adopted by the latter to counter this stress. It also highlights the effects of UV-B on plant phenolics and on various genes and enzymes of the phenylpropanoid pathway. Lastly, it touches upon the medicinal properties of various phenolic compounds and the futuristic studies to utilise UV-B as a potent elicitor of pharmacologically important phenolics.

Key Words : Human health; phenolic compounds; phenylpropanoid pathway; UV-B radiation

Abbreviations : 6,4-PPs- 6,4-photoproducts; ANS- anthocyanidin synthase; CFC- chlorofluorocarbon; CHS- chalcone synthase; CPDs- cyclobutane pyrimidine dimers; DFR- dihydroflavonol reductase; F3H- flavanone-3-hydroxylase; HCFC- hydrochlorofluorocarbon; IFR- isoflavone reductase; IFS- isoflavone synthase; ODSs- ozone depleting substances; PAL-phenylalanine ammonia lyase; ROS-reactive oxygen species; UV-B- ultraviolet-B

1. Introduction

Solar energy is the key to life on Earth. Ultraviolet (UV) radiation of the solar spectrum has been conventionally divided into UV-A (320-400 nm), UV-B (280-320 nm), and UV-C (less than 280 nm) of which UV-A and longer wavelengths of UV-B are of biological significance. Depletion of the stratospheric ozone layer has caused higher levels of UV-B radiation reaching the Earth. Since higher plants lack locomotion and cannot move away from sunlight, they have developed mechanisms and structures to adapt to the changes caused by the surplus UV-B radiation reaching them. One such strategy is the production of higher amounts of phenolics which act as

screening compounds and protect against oxidative damage due to UV-B. Since these compounds are synthesized via phenylpropanoid pathway, they are also called phenylpropanoid compounds. The studies on these compounds have revealed them to be vital factors for plant adaptation and survival and also from the perspective of human health. Hence, the objective of the present review is to highlight the importance of UV-B in eliciting these compounds in plants.

2. Stratospheric Ozone Layer and UV-B Scenario

The first reports on the stratospheric ozone depletion due to anthropogenic emissions of chlorofluorocarbons were put forward by Molina and Rowland in 1974 while the first documentation of the Antarctic ozone hole was made by Farman *et al* in 1985. Very soon after these alarming indications, Montreal Protocol on Substances that Deplete Ozone Layer was signed in 1987 to contain and limit the emission of ozone depleting substances (ODSs), which, according to the studies up to 2013 by Chipperfield *et al* (2015), has been quite effective in controlling ODSs emissions. Antarctic ozone hole was initially expected to recover by ~2050 obliterating UV-B as a potent stress factor influencing life on Earth. However, some studies prior to 2013 as well as some later ones depict a not-so-simple scenario. For instance, in 2012, Anderson *et al* found a link between changing climatic conditions and increased incidence of UV-B reaching the Earth due to increase in the frequency and intensity of thunderstorms which are capable of thrusting water molecules into the air up to the stratosphere whence the sulphate aerosols attract these molecules, and chemical reactions occur which destroy ozone. Bornman *et al* (2015) have in turn demonstrated that carbon release from the plant litter and soils due to UV-B might be instrumental in contributing to global warming. Moreover, Laube *et al* (2014) have detected and quantified three CFCs and one HCFC with unknown emission sources which are being destroyed very slowly in the atmosphere and may be instrumental in increased levels of UV-B reaching the Earth. Already, in 2006, predictions have been made that full ozone hole recovery is expected to occur by 2068 (as against 2050 as previously expected), and a significant decrease in the area in not expected to start to occur until about 2024 (Newman *et al*, 2006). More recently, NASA scientists have predicted the ozone-hole size to return to pre-1980 levels by about 2075 (NASA, 2015). Since the ozone hole depletion and UV-B levels are directly related, despite the restrictions on ODSs, UV-B is still considered a threat to all living organisms.

3. Plant Responses to UV-B: Effects and Counteractive Protective Measures

Photosynthesis is a vital process in plants which requires sunlight; consequently, plants are inevitably exposed to UV-B radiation as well. Plants may respond both positively and negatively to the environment and the stresses they encounter. High levels of UV-B are capable of influencing various aspects of plants like morphology, physiology, biochemistry, and molecular biology. The effects of UV B on plants are highly varied depending upon a number of factors like species and cultivar sensitivity, growth chamber, greenhouse, or open field conditions, season of

growth, the intensity and duration of UV B exposure (according to the type of UV lamps used), exposure system and set up, as well as the availability of visible light, and the action spectra used for computing biologically effective UV B radiation (Runeckles and Krupa, 1994; Jordan, 1996).

Bronzing and glazing are the initial symptoms observed upon exposure of plants to s-UV-B, while chronic exposure to this stress results in chlorosis, necrosis, leaf desiccation and their early senescence (Strid and Porra, 1992; Reddy *et al*, 2003; Demkura *et al*, 2010). Glazing (due to the accumulation of waxy compounds; Teramura, 1983) and bronzing (possibly due to the accumulation of coloured pigments such as carotenoids and anthocyanins or due to oxidation of phenolic compounds; Teramura, 1983; Cline and Salisbury, 1996) can be regarded as defence mechanisms against UV-B as the plant tries to attenuate this radiation and prevent its excessive penetration into the leaf interior. Other symptoms such as leaf curling and cupping (due to partial destruction of the growth hormone indole acetic acid on the exposed surface) have been observed in *Cyanoglossum officinale* (Furness *et al*, 1999), *Avena sativa* and *Setaria viridis* (Zuk-Golaszewska *et al*, 2003), and *Passiflora edulis* (Cechin *et al*, 2012). This reduces the exposed leaf surface area to UV-B as a protective measure. Increase in leaf thickness, changes in the number and size of palisade and spongy parenchyma cells and decreased stomatal frequency are some of the common plant responses to UV-B (Bornman and Vogelmann, 1991; Lingakumar and Kulandaivelu, 1993; Weston *et al*, 2000). This might be due to addition of spongy mesophyll cells and/or due to lengthening of palisade parenchyma cells or increased number of palisade parenchyma layers (Weston *et al*, 2000) and are instrumental in attenuating the penetration of UV-B radiation into the leaf.

Generalised morphological changes due to s-UV-B include reductions in plant height, leaf area, plant biomass, delayed seedling and flower emergence, alterations in biomass accumulation patterns, and reductions in crop yield. However, a number of studies with dissimilar results have been reported (Reviewed by Kakani *et al*, 2003). At the biochemical level, major changes caused by UV-B include enhanced production of reactive oxygen species (ROS) (capable of causing peroxidation of lipids, protein oxidation, and impairment of nucleic acids and enzymatic activities; Mishra *et al*, 2011), DNA damage (either direct via formation of cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6-4) pyrimidone dimers (6,4-PPs) (Britt, 1996), or indirectly via ROS), damage to the photosynthetic apparatus (including pigments, thylakoid membrane, stomatal parameters, Rubisco, cytochrome b/f-, light harvesting-, and PSI- and PSII complexes; Strid *et al*, 1994; Nogués and Baker, 1995; Nogués *et al*, 1999), and production of secondary metabolites.

ROS induced oxidative stress is countered by various enzymatic and non-enzymatic antioxidants in plants which either directly scavenge ROS (e.g. superoxide dismutase) or utilize various molecules such as flavonoids and ascorbate as substrates (e.g. peroxidases) to achieve the same results (Noctor and Foyer, 1998). To counteract DNA damage due to UV-B, three basic photorepair mechanisms come into play,

photoreactivation, excision, and recombinational repair (Britt, 1995; Taylor *et al.*, 1996), while damage to the photosynthetic apparatus are countered by synthesizing new enzymes and proteins in lieu of the damaged ones, repairing the chloroplastic DNA, and restoring D1 and D2 protein activities (if only partially) (Greenberg *et al.*, 1989a, b; Wilson and Greenberg, 1993), and synthesizing and accumulating phenolic compounds (Jansen and Van Den Noort, 1998). Hence, biosynthesis of various phenolic compounds and flavonoids serve both UV-B screening and UV-B defence functions.

Prior to their recognition as essential compounds in plant adaptation and survival, secondary metabolites (various phenolic compounds including phenolics and others) were considered to be ‘waste products’ of plants since they are not directly involved in plant growth and development. However, they are as vital as primary plant metabolites, if not more so, due to their roles in plant adaptation and survival. Some of their functions include attraction of insects as pollinators and seed dispersal agents, protection against herbivory, insect attacks and pathogens, as phytoalexins, UV-B screening compounds, and growth hormones, stimulation of root nodule formation, and as signalling compounds. They are also commercially important, being exploited for the production of dyes, drugs, artificial flavouring compounds, and perfumes amongst others (Bruneton, 1999; Heinrich *et al.*, 2004). Fig.1 generalises the functions of these compounds in plants.

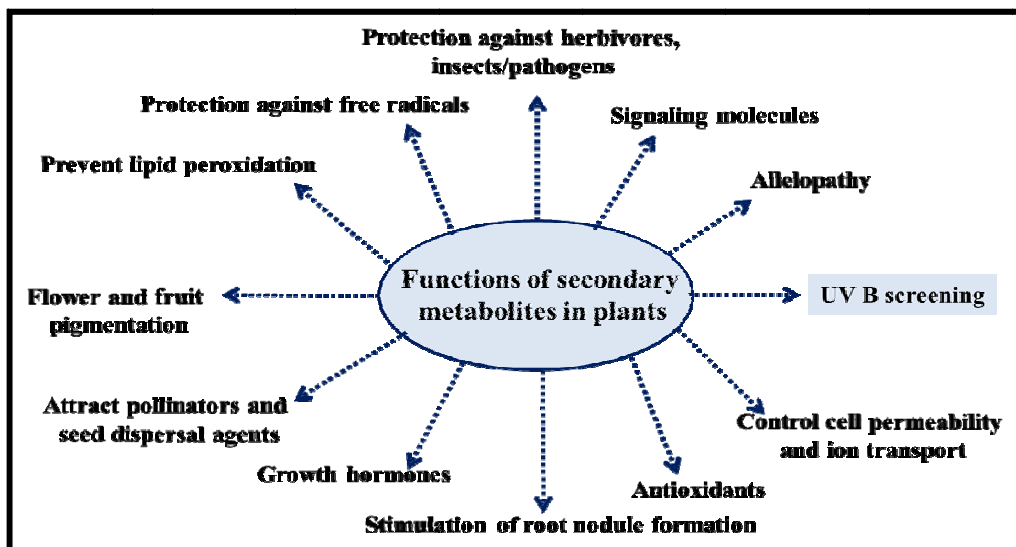


Fig.1. Generalized functions of secondary metabolites in plants

4. Effects of UV-B on Plant Phenolics

The phenylpropanoid pathway, leading to the production various categories of phenolic compounds, is omnipresent in plants. Phenolics comprise more than 10,000

structures known to date; flavonoids comprise the largest group of phenolics with more than 6000 members (Bowsher and Tobin, 2008). Their classification, based on that of Daniel (2006) is outlined in Fig. 2.

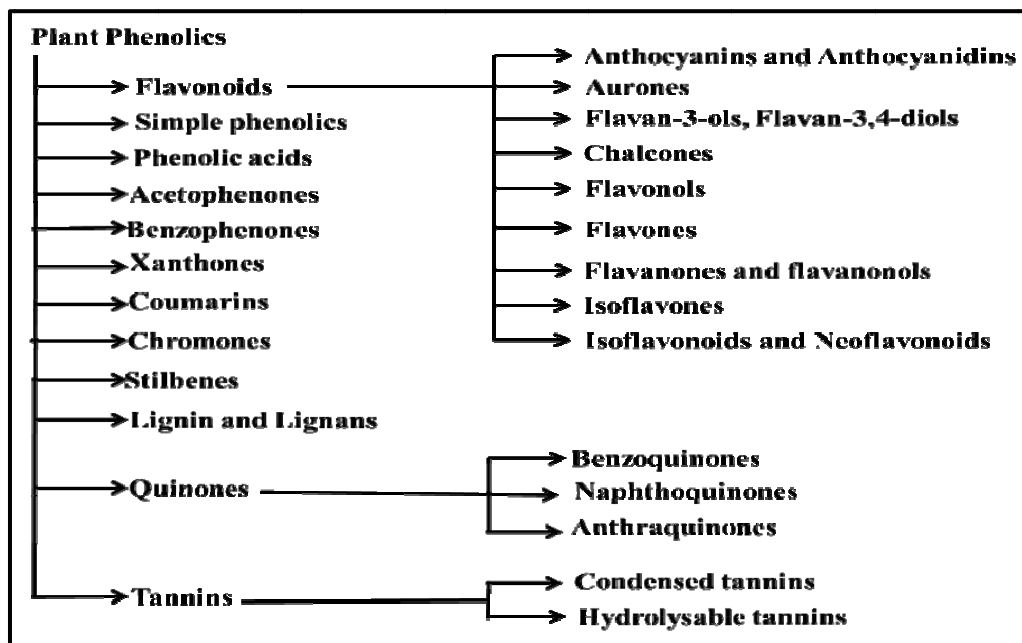


Fig.2. Classification of phenolic compounds synthesized via phenylpropanoid pathway (based on Daniel, 2006)

Both soluble and insoluble forms of plant phenolics absorb in the UV-B range and hence act as effective sunscreen pigments. The former are rapidly inducible upon UV-B exposure while the cell wall bound forms are more passively induced (Lavola *et al.*, 2003). Phenolic compounds also act as efficient ROS scavengers (Agati and Tattini, 2010; Fini *et al.*, 2011). Some other important functions of plant phenolics include stimulation of root nodule formation, offering disease resistance, regulating auxin transport and cell growth, and functioning as allelopathic agents (Koes *et al.*, 1994; Pierpoint, 2000; Chong *et al.*, 2009; Kuhn *et al.*, 2011). Some important categories of phenolic compounds studied under s-UV-B are given below.

Anthocyanins (sugar conjugates of anthocyanidins) may also form conjugates with hydroxycinnamates and organic acids. They have been known to accumulate under low fluence UV-B in crops such as maize, rice, apple, rose, and *Arabidopsis* (referenced in Guo *et al.*, 2008). Anthocyanins are believed to increase the antioxidant potential of plants in order to uphold the balanced physiological status in tissues under UV-B stress. In several medicinal/fruited cultivars, anthocyanin accumulation is induced by light in the UV-B region (280-320nm wavelength range) when applied in combination with solar infrared radiation (Arakawa, 1988).

Flavonols, a category of flavonoids occurring as O-glycosides have been found to increase upon exposure to UV-B. Common examples include myricetin, quercetin, and kaempferol and their derivatives. Quercetin glycosides and kaempferol 3-rhamnoside enhanced upon UV-B exposure in the leaves of silver birch while myricetin content remained unchanged (Tegelberg *et al*, 2001). More recently, both quercetin and kaempferol concentrations were found to be increased under elevated UV-B levels in young broccoli plants by Kuhlmann and Müller (2009), mung bean cultivars HUM1 and HUM12 and pea cultivars HUP2 and HUDP15 by Choudhary and Agrawal (2014a, b). It has also been hypothesised that quercetin flavonols are better able to scavenge free radicals than kaempferol flavonols and hence quercetin/kaempferol ratio is highest in UV-B exposed plants for better protection against oxidative stress (Harborne and Williams, 2000). Moreover, UV-B exclusion studies conducted on strawberries revealed reduced concentrations of flavonols quercetin 3-glucuronide and kaempferol 3-glucoside and also that of anthocyanin cyanidin 3-glucoside (Josuttis *et al*, 2010). Exposure to UV-B causes the accumulation of these compounds in the epidermal layers of exposed plant organs where they act as filters denying excessive light penetration to the internal tissues and organs (Wilson *et al*, 1998). Flavones (closely resembling flavonols) also function in the same vein.

Flavonoids in general were found to be increased in a number of plants upon exposure to elevated UV-B levels, for instance, in leafy salad plant *Gynura bicolor* (Schirrmacher *et al*, 2004), *Vitis vinifera* (Majer and Hideg, 2012), *Raphanus sativus* (Singh *et al*, 2012), *Hordeum vulgare* (Klem *et al*, 2012), and mung bean and pea cultivars (Choudhary and Agrawal, 2014a, b) to cite a few. Flavonoids act as stabilizers and protectors of the lipid phase of the thylakoid membrane and act as quenchers of triplet (excited) state chlorophyll and singlet oxygen generated under oxidative stress (Agrawal and Rathore, 2007). A UV-B exclusion study conducted on some phenolic acids (caffeic acid, *p*-coumaric acid and ferulic acid) in tomato found them to be 20% lower when grown under complete UV-B exclusion (Luthria *et al*, 2006). Coumarins and furanocoumarins absorb strongly in the UV wavebands and increase with enhanced UV B radiation in *Pastinaca sativa* (Zangerl and Berenbaum, 1987).

Postharvest supplementary UV-B application can also increase the concentration of various phenolic compounds. UV-B dose of about $0.5 \text{ KJ m}^{-2} \text{ d}^{-1}$ increased flavonols and phenolic acids (hydroxycinnamic and hydro-xybenzoic acids) in black currant and white asparagus spears (Huyskens-Keil *et al*, 2007). Furthermore, increasing postharvest UV-B dosages enhanced concentrations of quercetin in onion (Higashio *et al*, 2005) and increased anthocyanin levels in peach, apples and strawberry (Marais *et al*, 2001; Kataoka and Beppu, 2004; Higashio *et al*, 2005). In berry fruits, anthocyanins were reported to increase after UV irradiation within a short time (Huyskens-Keil *et al*, 2007), whereas in UV-B treated apples, increased synthesis of flavonols was faster and flavonol accumulation was higher in comparison to anthocyanins (Ban *et al*, 2007; Hagen *et al*, 2007). These findings indicate that

flavonols might have a greater impact on antioxidant protection against UV-B. Interestingly, antioxidant activity was highly correlated with the UV-B mediated increase in flavonoid pattern of berry and apple fruits (Hagen *et al*, 2007; Huyskens-Keil *et al*, 2007).

Other end-products of the phenylpropanoid pathway such as lignin are also influenced by UV-B radiation. UV-B causes changes in the lignin content and composition of plants (Rozema *et al*, 1997). Increased epidermal wall thickness due to enhanced lignin deposition was observed by Hilal *et al* (2004) in *Chenopodium quinoa* cotyledons, Yamasaki *et al* (2007) in trichomes of *Cucumis sativus* cotyledons and Tripathi and Agrawal (2013) in *Linum usitatissimum* L. Tannin concentrations were found to be unaffected or negatively affected by UV-B radiation (Kreft *et al*, 2002; Lavola *et al*, 2003) which signifies that plants synthesize only those compounds which are important safeguards against UV-B stress (de la Rosa *et al*, 2001). However, Germ *et al* (2010) reported an increase in tannin content in leaves of *Hypericum perforatum*.

5. Genes and Enzymes of Phenylpropanoid Pathway as Influenced by UV-B

The enzymes and products of the phenylpropanoid pathway (leading to a vast array of phenolic compounds) are the most widely studied under UV-B influence. As reported in the previous section, UV-B has been known to increase the concentration of flavonoids (and its subgroups like anthocyanins, flavonols, chalcones), stilbenes, lignin, and tannins in a number of plant species. Enzymes such as PAL (phenylalanine ammonia lyase, catalysing the transformation of phenylalanine to *trans*-cinnamic acid), CHS (chalcone synthase, which catalyses the first committed step of this pathway utilising malonyl CoA and 4-coumaroyl CoA to produce chalcones), IFS (isoflavone synthase, involved in plant defence and root nodulation), IFR (isoflavone reductase, responsible for phytoalexin biosynthesis involved in plant defence), DFR (dihydroflavonol reductase, first enzyme in the pathway committed to anthocyanin biosynthesis), F3H (flavanone-3-hydroxylase, necessary for the production of both flavonols and anthocyanins), and other enzymes have been studied under UV-B and have been found to be usually up-regulated in plants such as lettuce, *Phaseolus trilobus* (wild gram), and *Ligustrum vulgare* (common privet) (Tomas-Barberan and Espin, 2001; Treutter, 2005; Park *et al*, 2007; Ravindran *et al*, 2010; Agati *et al*, 2011 and references therein). Anthocyanin biosynthetic pathway enzymes have also been reported to be triggered by UV-B radiation in *Arabidopsis* (Fuglevand *et al*, 1996). The elevated levels of transcripts of PAL, DFR, and ANS (anthocyanidin synthase) were accompanied by an increase in the anthocyanin pigments (Guo *et al*, 2008). Ubi *et al* (2006) reported an increased accumulation of anthocyanin pigments in apple fruit skin by inducing the expression of anthocyanin biosynthetic genes, especially chalcone synthase, anthocyanidin synthase, and anthocyanin-3-O-glucosyl transferase genes. A series of involved enzymes, such as phenylalanine ammonia lyase, cinnamate-4-hydroxylase, p-coumaroyl-CoA ligase and stilbene synthase involved in resveratrol synthesis were shown to be upregulated by UV-B irradiation in grape berries (Li *et al*, 2008).

6. Phenolic Compounds and Benefits for Human Health

Initially, secondary plant metabolites were dismissed as anti-nutritive plant substances in terms of human nutrition. However, the importance of secondary plant metabolites for human nutrition has been reconsidered due to the discovery of their protective potential and health-promoting benefits that range from the stimulation of antioxidative mechanisms to a reduced risk of cancer incidence and cardiovascular disease (Watzl and Leitzmann, 2005). Amongst all plant secondary metabolites, phenylpropanoids are considered to be of immense biological importance because of their antioxidant properties. This property enables them to be utilized as important constituents of human diet from nutritional and health perspective. For instance, polyphenolic antioxidants may help reduce incidence of cancer, cardiovascular and neurodegenerative diseases, prevent DNA damage and may be involved in anti-ageing, preventing age-related disorders (Obrenovich *et al*, 2010). Hollman and Katan (1999) have found that intake of flavonols and flavones were inversely associated with subsequent coronary heart disease in most of the studies they reviewed. The general public has become increasingly aware of and concerned about overall food quality (Schreiner, 2009), therefore an interesting possibility is to exploit UV-B induced metabolic changes in fruit, vegetables and herbs to satisfy consumer demand for natural health-promoting food products. Some of the common categories of phenolic compounds and their health benefits/ medicinal properties are outlined in Table 1.

Table 1. Some important categories of phenolic compounds and their medicinal properties

Phenolic compounds	Medicinal Properties	References
(i) Flavonoids:	Anticancer, anti-viral, anti-allergic, anti-stress, estrogenic antibiotic, antioxidant, antidiarrheal, antiulcer, anti-inflammatory	Sharma 2006, Lu <i>et al</i> 2006, Agrawal 2011
a. Anthocyanins and Anthocyanidins	Antioxidant, anti-platelet, chemopreventive, antimicrobial, anticarcinogenic, proapoptotic, neuroprotective, cardioprotective, anti-hepatotoxic, anti-lipolytic, vasodilatory, enhance memory	Hollman and Katan 1999, Scalbert <i>et al</i> 2005, Youdim 2002; Luciola 2012
b. Flavonols	Anti-mutagenic, antioxidant, antimicrobial, anti-carcinogenic, anti-hypertensive, anti-allergic, anti-depressant, anti-diabetic, enzyme-inhibitors, neuroprotective, cardioprotective, chemopreventive,	Bohm 1998, Bruneton 1999 Cai <i>et al</i> 2004, Goutam and Dilip 2006
c. Flavones	Anti-tuberculosis, anti-microbial, anti-tumour, antioxidant, anti-carcinogenic, anti-inflammatory, anti-proliferative, anti-angiogenic, anti-estrogenic, improvement of blood circulation	Bohm 1998, Bruneton 1999, Havsteen 2002, Huang <i>et al</i> , 2009, Kashani <i>et al</i> 2012

d. Flavanones and flavanonols	Antioxidant, antiproliferative, estrogenic, radio-protective, anti-inflammatory, analgesic, anti-hypercholesterolemic, anti-carcinogenic, antimicrobial, hepatoprotective, CNS depressants	Bruneton 1999, Pietta 2000, Tamilselvam <i>et al</i> 2013
(ii) Phenolic acids	Anticancer, cardio-protective, anti-ulcer, cytotoxic, antioxidant, antiseptic, antimicrobial, anti-inflammatory, anti-tumour, anti-spasmodic, anti-depressant, treatment of dyspepsia	Dalen 2006, Cai <i>et al</i> 2004, Luk <i>et al</i> 2007, Surveswaran <i>et al</i> 2007
(iii) Coumarins	anthelmintic, anti-asthmatic, anti-coagulant, anti-tumour, anti-viral, anti-inflammatory, anti-oxidant, anti-microbial and enzyme-inhibitory, anti-obesity, anti-mutagenic, digestive, astringent, stomachic, heart tonic, hypoglycaemic, spasmolytic, vasodilators	Daniel 2006, Kontogiorgis <i>et al</i> 2007, Borges <i>et al</i> 2009
(iv) Stilbenes	Chemoprotective, anticancer, antioxidant, anti-ageing, anti-angiogenic, neuroprotective, anti-fungal, immune modulation	Shankar <i>et al</i> 2007, Zykova <i>et al</i> 2008, Zhang and Björn 2009, Kasiotis <i>et al</i> 2013
(v) Lignans	Antimicrobial, antioxidant, anti-inflammatory, anti-cancer, antiviral, anti-pyretic, diuretic, analgesic, anti-rheumatic, anti-neoplastic, phytoestrogenic, cathartic, immunosuppressive, hepato-protective, cardio-protective, treatment of osteoporosis, rheumatoid arthritis, gastric and duodenal ulcers	Bernhoft 2010, Nagar <i>et al</i> 2011
(vi) Quinones:		
a. Benzoquinones	Antioxidant, anti-inflammatory, anti-cancer, treatment of mitochondrial diseases, prevent atherosclerosis, retinal cell apoptosis	Perez-Sanchez <i>et al</i> 2012, Lulli <i>et al</i> 2012, Skulachev <i>et al</i> 2009
b. Naphthoquinones	Antibiotic, anti-viral, anti-inflammatory, anti-pyretic, anti-proliferative, cytotoxic, anti-allergic, anti-asthmatic	Romanova <i>et al</i> 1978, Babula <i>et al</i> 2009
c. Anthraquinones	Anti-inflammatory, anti-depressant, antimicrobial, anti-dermatic, anthelmintic, purgative, tonic, treatment of gout, rheumatism, leukaemia, responsible for peristaltic colon movement and water and electrolyte secretion	Duke 1985, Cai <i>et al</i> 2006, Huang <i>et al</i> 2007
(vii) Tannins :		
a. Condensed tannins	Antioxidant, anti-cancer, anti-HIV, anti-diarrhoea, anti-inflammatory, antibacterial	Gurib-Fakim 2006, Kashani <i>et al</i> 2012
b. Hydrolysable tannins	Anti-diarrhoea, antidote in poisoning by heavy metals	Heinrich <i>et al</i> 2004, Bernhoft 2010, Kashani <i>et al</i> 2012

7. Challenges and Future Perspectives

Certain difficulties might be encountered while inducing secondary metabolite(s) via UV B radiation. UV B alters the concentration of not only the desired compound but the overall secondary metabolite profile (Schreiner *et al*, 2009). Also, some compounds may not necessarily respond favourably to UV B radiation (Schmidt *et al*, 2011). In addition, UV B induced changes in plant secondary metabolite concentration may synergistically or antagonistically affect levels of other primary and secondary metabolites. The bioavailability of the desired compound may also prove to be an issue. Accurate assessment of bioavailability in humans is difficult, expensive, and time-consuming. However, validated cell culture models can also be used to assess bioavailability in a cost-effective and rapid manner (Aherne *et al*, 2009; O'Sullivan *et al*, 2010).

The consumption of secondary metabolites above the toxicity threshold may have potential adverse health consequences. Therefore, studies involving detailed evaluation of these compounds, along with exhaustive dose-response studies need to be performed to better understand the roles of the desired compounds in foods and nutraceuticals of human diet (Son *et al*, 2008). Hence, UV B induced changes in plant metabolome call up meticulous researches in both animal as well as human models.

In the usage of plants for bio-manufacturing purposes, the production and isolation of single secondary plant metabolites in nutraceuticals can be promoted via UV B radiation if a detailed and intricate knowledge of the key regulatory steps of the biosynthetic pathway are known. The dose of the stress can also be optimised to yield the enhanced concentration of the desired secondary metabolite (Schreiner and Huyskens-Keil, 2006; Schreiner *et al*, 2009, 2011). Clearly, the use of UV B radiation to improve the nutritional quality of food products is likely to be a case of 'precision manipulation' whereby UV doses, accumulation dynamics, other environmental parameters, genotype and cell regulatory steps will all need to be considered and regulated simultaneously to achieve the desired results.

Acknowledgements: The authors are thankful to the Head, and to the Coordinator, Centre of Advanced Study, Department of Botany, Banaras Hindu University, for providing laboratory facilities for a part of our research related to this review and to University Grants Commission (UGC), New Delhi, for financial assistance in the form of Junior- and Senior Research Fellowships.

References

- Agati G, Biricolli S, Guidi L, Ferrini F, Fini A, Tattini M, 2011. The biosynthesis of flavonoids is enhanced similarly by UV radiation and root zone salinity in *L. vulgare* leaves. *Journal of Plant Physiology*, 168: 204-212.
- Agati G, Tattini M, 2010. Multiple functional roles of flavonoids in photoprotection. *New Phytologist*, 186: 786-793.

- Agrawal AD, 2011. Pharmacological activities of flavonoids: A review. *International Journal of Pharmaceutical Sciences and Nanotechnology*, 4: 1394-1398.
- Agrawal SB, Rathore D, 2007. Changes in oxidative stress defense system in wheat (*Triticum aestivum* L.) and mung bean (*Vigna radiata* L.) cultivars grown with and without mineral nutrients and irradiated by supplemental ultraviolet-B. *Environmental and Experimental Botany*, 59: 21-33.
- Aherne SA, Jiwan MA, Daly T, O'Brien NM, 2009. Geographical location has greater impact on carotenoid content and bioaccessibility from tomatoes than variety. *Plant Foods and Human Nutrition*, 64: 250-256.
- Anderson JG, Wilmouth DM, Smith JB, Sayers DS, 2012. UV dosage levels in summer: increased risk of ozone loss from convectively injected water vapour. *Science*, 337: 835-839.
- Arakawa O, 1988. Photo-regulation of anthocyanin synthesis in apple fruit under UV-B and red light. *Plant and Cell Physiology* 29: 1385-1389.
- Babula P, Adam V, Havel L, Kizek R, 2009. Noteworthy secondary metabolites naphthoquinones- their occurrence, pharmacological properties and analysis. *Current Pharmaceutical Analysis*, 5: 47-58.
- Ban Y, Honda C, Bessho H, Pang XM, Moriguchi T, 2007. Suppression subtractive hybridization identifies genes induced in response to UV-B irradiation in apple skin: isolation of a putative UDP-glucose 4-epimerase. *Journal of Experimental Botany*, 58: 1825-1834.
- Bernhoft A, 2010. A brief review on bioactive compounds in plants. In: Bernhoft A (Ed): *Bioactive Compounds in Plants- benefits and risks for man and animals*. Oslo: The Norwegian Academy of Science and Letters, pp. 11-17.
- Bohm B, 1998. *Introduction to flavonoids*. Amsterdam: Harwood Academic Publishers.
- Borges F, Roleira F, Milhazes N, Uriarte E, Santana L, 2009. Simple coumarins: Privileged scaffolds in medicinal chemistry. *Frontiers in Medicinal Chemistry*, 4: 23-85.
- Bornman JF, Barnes PW, Robinson SA, Ballaré CL, Flint SD, Caldwell MM, 2015. Solar ultraviolet radiation and ozone depletion driven climate change: effects on terrestrial ecosystems. *Photochemical and Photobiological Sciences*, 14: 88-107.
- Bornman JF, Vogelmann TC, 1991. Effect of UV-B radiation on leaf optical properties measured with fiber optics. *Journal of Experimental Botany*, 41: 547-554.
- Bowsher CS, Tobin M, 2008. *Plant Biochemistry A*. Garland Science, New York.
- Britt AB, 1995. Repair of DNA damage induced by ultraviolet radiation. *Plant Physiology*, 108: 891-896.
- Britt AB, 1996. DNA damage and repair in plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 47: 75-100.
- Bruneton J, 1999. *Pharmacognosy, Phytochemistry and Medicinal Plants*. Intercept. Ltd. England, U.K.
- Cai YZ, Luo Q, Sun M, Corke H, 2004. Antioxidant activity and phenolic compounds of 112 traditional Chinese medicinal plants associated with anticancer. *Life Sciences*, 74: 2157-2184.

- Cai YZ, Sun M, Xing J, Luo Q, and Corke H, 2006. Structure-radical scavenging activity relationships of phenolic compounds from traditional Chinese medicinal plants. *Life Science*, 78: 2872-2888.
- Cechin I, Rocha VJ, Fumis TF, 2012. Sensitivity of yellow passion fruit to ultraviolet-B radiation. *Pesquisa Agropecuária Brasileira*, Brasília, 47: 1422-1427.
- Chipperfield MP, Dhomse SS, Feng W, McKenzie RL, Velders GJM, Pyle JA, 2015. Quantifying the ozone and ultraviolet benefits already achieved by the Montreal Protocol. *Nature Communications*, 6: 7233, doi: 10.1038/ncomms8233.
- Chong J, Poutaraud A, Huguency P, 2009. Metabolism and roles of stilbenes in plants. *Plant Science*, 177: 143-155.
- Choudhary KK, Agrawal SB, 2014a. Cultivar specificity of tropical mung bean (*Vigna radiata* L.) to elevated ultraviolet-B: Changes in antioxidative defense system, nitrogen metabolism and accumulation of jasmonic and salicylic acids. *Environmental and Experimental Botany*, 99: 122-132.
- Choudhary KK, Agrawal SB, 2014b. Ultraviolet-B induced changes in morphological, physiological, and biochemical parameters of two cultivars of pea (*Pisum sativum* L.). *Ecotoxicology and Environmental Safety*, 100: 178-187.
- Cline MG, Salisbury FB, 1996. Effects of ultraviolet radiation on leaves of higher plants. *Radiation Botany*, 6: 151-163.
- Dalen JE, 2006. Aspirin to prevent heart attack and stroke: what's the right dose? *American Journal of Medicine*, 119: 198-202.
- Daniel M, 2006. *Medicinal Plants: Chemistry and Properties*. Science Publishers, USA.
- de la Rosa TM, Julkunen-Tiitto R, Lehto T, Aphalo PJ, 2001. Secondary metabolites and nutrient concentrations in silver birch seedlings under five levels of daily UV-B exposure and two relative nutrient addition rates. *New Phytologist*, 150: 121-131.
- Demkura PV, Abdala G, Baldwin IT, Ballaré CL, 2010. Jasmonate-dependent and -independent pathways mediate specific effects of solar ultraviolet B radiation on leaf phenolics and antiherbivore defense. *Plant Physiology*, 152: 1084-1095.
- Duke JA, 1985. *Handbook of medicinal herbs*. CRC Press, Boca Raton, Florida.
- Farman JC, Gardiner BG, Shanklin JD, 1985. Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature*, 315: 207-210.
- Fini A, Brunetti C, Di Ferdinando M, Ferrini F, Tattini M, 2011. Stress-induced flavonoid biosynthesis and the antioxidant machinery of plants. *Plant Signaling and Behavior*, 6: 709-711.
- Fuglevand G, Jackson JA, Jenkins GI, 1996. UV B, UV A, and blue light signal transduction pathways interact synergistically to regulate chalcone synthase gene expression in *Arabidopsis*. *Plant Cell*, 8: 2347-2357.
- Furness NH, Upadhyaya MK, Ormrod DP, 1999. Seedling growth and leaf surface morphological responses of three rangeland weeds to ultraviolet-B radiation. *Weed Science*, 47: 427-434.
- Germ M, Stibilj V, Kreft S, Gaberščik A, Kreft I, 2010. Flavonoid, tannin and hypericin concentrations in the leaves of St. John's wort (*Hypericum perforatum* L.) are affected by UV-B radiation levels. *Food Chemistry*, 122: 471-474.

- Goutam B, Dilip G, 2006. Progress in the research on naturally occurring flavones and flavonols: An overview. *Current Organic Chemistry*, 10: 873-898.
- Greenberg BM, Gaba V, Canaani O, Malkin S, Mattoo AK, Edelman M, 1989a. Separate photosensitizers mediate degradation of the 32kDa photosystem II reaction center protein in the visible and UV spectral regions. *Proceedings of the National Academy of Sciences of the United States of America*, 86: 6617-6620.
- Greenberg BM, Gaba V, Mattoo AK, Edelman M, 1989b. Degradation of the 32kDa photosystem II reaction center protein in UV, visible, and far red light occurs through a common 23.5kDa intermediate. *Zeitschrift für Naturforschung*, 44: 450-452.
- Guo J, Han W, Wang M, 2008. Ultraviolet and environmental stresses involved in the induction and regulation of anthocyanin biosynthesis: A review. *African Journal of Biotechnology*, 7: 4966-4972.
- Gurib-Fakim A, 2006. Medicinal plants: Traditions of yesterday and drugs of tomorrow. *Molecular Aspects of Medicine* 27: 1-93.
- Hagen SF, Borge GIA, Bengtsson GB, Bilger W, Berge A, Haffner K, Solhaug KA, 2007. Phenolic contents and other health and sensory related properties of apple fruit (*Malus domestica* Borkh., cv. Aroma): Effect of postharvest UV-B irradiation. *Postharvest Biology and Technology*, 45: 1-10.
- Harborne JB, Williams CA, 2000. Advances in flavonoid research since 1992. *Phytochemistry* 55: 481-504.
- Havsteen BH, 2002. The biochemistry and medical significance of the flavonoids. *Pharmacology and Therapeutics*, 96: 67-202.
- Heinrich M, Barnes J, Gibbons S, Williamson EM, 2004. *Fundamentals of Pharmacognosy and Phytotherapy*. Churchill Livingstone, Elsevier Science Ltd., UK.
- Higashio H, Hirokane H, Sato F, Tokuda S, Uragami A, 2005. Effect of UV irradiation after the harvest on the content of flavonoid in vegetables. *Acta Horticulturae*, 682: 1007-1012.
- Hilal M, Parrado MF, Rosa M, Gallardo M, Orce L, Marta Massa E, González JA, Prado FE, 2004. Epidermal lignin deposition in quinoa cotyledons in response to UV-B radiation. *Photochemistry and Photobiology*, 79: 205-210.
- Hollman PC, Katan MB, 1999. Health effects and bioavailability of dietary flavonols. *Free Radical Research*, 31: 75-80.
- Huang Q, Lu G, Shen HM, Chung MC, Ong CN, 2007. Anti-cancer properties of anthraquinones from rhubarb. *Medicinal Research Reviews*, 27: 609-630.
- Huang W, Cai Y, Zhang, Y, 2009. Natural Phenolic compounds from medicinal herbs and dietary plants: Potential use for cancer prevention. *Nutrition and Cancer*, 62: 1-20.
- Huyskens-Keil S, Eichholz I, Kroh LW, Rohn S, 2007. UV-B induced changes of phenol composition and antioxidant activity in black currant fruit (*Ribes nigrum* L.). *Journal of Applied Botany and Food Quality*, 81: 140-144.
- Jansen MAK, Van Den Noort ER, 1998. Higher plants and UV-B radiation: balancing damage, repair and acclimation. *Trends in Plant Science*, 3: 131-135.
- Jordan BR, 1996. The effects of ultraviolet-B radiation on plants: a molecular perspective. *Advances in Botanical Research*, 22: 97-162.

- Josuttis M, Dietrich H, Treutter D, Will F, Linnemannstons L, Kruger E, 2010. Solar UVB responses of bioactives in strawberry (*Fragaria X ananassa* Duch. L.): a comparison of protected and open-field cultivation. *Journal of Agricultural and Food Chemistry*, 58: 12692-12702.
- Kakani VG, Reddy KR, Sailaja K, 2003. Field crop responses to ultraviolet B radiation: a review. *Agricultural and Forest Meteorology*, 120: 191-218.
- Kashani HH, Hoseini ES, Nikzad H, Aarabi MH, 2012. Pharmacological properties of medicinal herbs by focussing on secondary metabolites. *Life Science Journal* 9: 509-520.
- Kasiotis KM, Prtasinis H, Kletsas D, Haroutounian SA, 2013. Resveratrol and related stilbenes: Their anti-ageing and anti-angiogenic properties. *Food and Chemical Toxicology*, 61: 112-120.
- Kataoka I, Beppu K, 2004. UV irradiance increases development of red skin color and anthocyanins in 'Hakuho' peach. *HortScience*, 39: 1234-1237.
- Klem K, Alexander AC, Holuba P, Kovca D, Spundaa V, Robsonb M, Urbana O, 2012. Interactive effects of PAR and UV radiation on the physiology, morphology and leaf optical properties of two barley varieties. *Environmental and Experimental Botany*, 75: 52- 64.
- Koes RE, Quattrocchio F, Mol JNM, 1994. The flavonoid biosynthetic pathway in plants: function and evolution. *BioEssays*, 16: 123–132.
- Kontogiorgis CA, Xu Y, Hadjipavlou-Litina D, Luo Y, 2007. Coumarin derivatives protection against ROS production in cellular models of A β toxicities. *Free Radical Research*, 41: 1168-1180.
- Kreft S, Štrukelj B, Gaberščik A, Kreft I, 2002. Rutin in buckwheat herbs grown at different UV-B radiation levels: comparison of two UV spectrophotometric and an HPLC method. *Journal of Experimental Botany*, 53: 801–1804.
- Kuhlmann F, Müller C, 2009. Independent responses to ultraviolet radiation and herbivore attack in broccoli. *Journal of Experimental Botany*, 60: 3467-3475.
- Kuhn BM, Geisler M, Bigler L, Ring C, 2011. Flavonols accumulate asymmetrically and affect auxin transport in *Arabidopsis*. *Plant Physiology*, 156: 585-595.
- Lavola A, Aphalo PJ, Lahti M, Julkunen-Tiitto R, 2003. Nutrient availability and the effect of increasing UV-B radiation on secondary plant compounds in Scots pine. *Environmental and Experimental Botany*, 49: 49-60.
- Li X, Zheng X, Yan S, Li S, 2008. Effects of salicylic acid (SA), ultraviolet radiation (UV-B and UV-C) on trans-resveratrol inducement in the skin of harvested grape berries. *Frontiers of Agriculture in China*, 2: 77-81.
- Lingakumar K, Kulandaivelu G, 1993. Changes induced by ultraviolet-B radiation in vegetative growth, foliar characteristics and photosynthetic activities in *Vigna unguiculata*. *Australian Journal of Plant Physiology*, 20: 299-308.
- Lu J, Papp LV, Fang J, Rodriguez-Nieto S, Zhivotovsky B, Holmgren A, 2006. Inhibition of mammalian thioredoxin reductase by some flavonoids: implications for myricetin and quercetin anticancer activity. *Cancer Research*, 66: 4410-4418.
- Lucioli S, 2012. Anthocyanins: Mechanism of action and therapeutic efficiency. In: Capasso A (Ed.) *Medicinal Plants as Antioxidant agents: Understanding their mechanism of action and Therapeutic efficacy*, Research Signpost, Kerela, India, pp: 27-57.

- Luk JM, Wang X, Liu P, Wong KF, Chan KL, Tong Y, Hui CK, Lau GK, Fan ST, 2007. Traditional Chinese herbal medicines for treatment of liver fibrosis and cancer: from laboratory discovery to clinical evaluation. *Liver International*, 27: 879-890.
- Lulli M, Witort E, Papucci L, Torre E, Schipani C, Bergamini C, Dal Monte M, Capaccioli S, 2012. Coenzyme Q10 instilled as eye drops on the cornea reaches the retina and protects retinal layers from apoptosis in a mouse model of kainate-induced retinal damage. *Investigative Ophthalmology and Visual Science*, 53: 8295-8302.
- Luthria DL, Mukhopadhyay S, Krizek DT, 2006. Content of total phenolics and phenolic acids in tomato (*Lycopersicon esculentum* Mill.) fruits as influenced by cultivar and solar UV radiation. *Journal of Food Composition and Analysis* 19: 771-777.
- Majer P, Hideg É, 2012. Developmental stage is an important factor that determines the antioxidant responses of young and old grapevine leaves under UV irradiation in a greenhouse. *Plant Physiology and Biochemistry*, 50:15-23.
- Marais E, Jacobs G, Holcroft DM, 2001. Postharvest irradiation affects colour development in bicoloured pome fruit. *Acta Horticulturae*, 553: 569-570.
- Mishra S, Jha AB, Dubey RS, 2011. Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings. *Protoplasma*, 248: 565-577.
- Molina MJ, Rowland FS, 1974. Stratospheric sink for chlorofluoromethanes: chlorine atom-catalysed destruction of ozone. *Nature*, 249: 810-812.
- Nagar N, Jat RK, Sharan R, Verma S, Sharma D, Bansal K, 2011. Podophyllotoxin and their glycosidic derivatives. *Pharmacophore*, 2: 124-134.
- NASA, 2015. <http://svs.gsfc.nasa.gov/cgi-bin/details.cgi?aid=30602> (accessed on 9th Feb. 2016)
- Newman PA, Nash ER, Kawa SR, Montzka SA, 2006. When will the Antarctic ozone hole recover? *Geophysical Research Letters*, 33: L12814, doi: 10.1029/2005GL025232.
- Noctor G, Foyer CH, 1998. Ascorbate and glutathione: keeping active oxygen under control. *Annual Review of Plant Physiology and Plant Molecular Biology*, 49: 249-279.
- Nogués S, Allen DJ, Morison JIL, Baker NR, 1999. Characterization of stomatal closure by ultraviolet-B radiation. *Plant Physiology*, 121: 489-496.
- Nogués S, Baker NR, 1995. Evaluation of the role of damage to photosystem II in the inhibition of CO₂ assimilation in pea leaves on exposure to UV-B radiation. *Plant, Cell and Environment*, 18: 781-787.
- O'Sullivan L, Jiwan MA, Daly T, O'Brien NM, Aherne SA, 2010. Bioaccessibility, uptake and transport of carotenoids from peppers (*Capsicum* spp.) using the coupled in vitro digestion and human intestinal caco-2 cell model. *Journal of Agricultural and Food Chemistry*, 12: 5374-5379.
- Obrenovich ME, Nair NG, Beyaz A, Aliev G, Reddy VP, 2010. The role of polyphenolic antioxidants in health, disease, and ageing. *Rejuvenation research*, 13: doi: 10.1089/rej.2010.1043.
- Park JS, Choung MG, Kim JB, Hahn BS, Kim JB, Bae SC, Roh KH, Kim YH, Cheon CI, Sung MK, Cho KJ, 2007. Genes upregulated during red colouration in UV B irradiated lettuce leaves. *Plant Cell Reports*, 26: 507-516.

- Perez-Sanchez C, Ruiz-Limon P, Aguirre MA, Bertolaccini ML, Khamashta MA, Rodriguez-Ariza A, Segui P, Collantes-Estevez E, Barbarroja N, Khraiwesh H, Gonzalez-Reyes JA, Villalba JM, Velasco F, Cuadrado MJ, Lopez-Pedraza C, 2012. Mitochondrial dysfunction in antiphospholipid syndrome: implications in the pathogenesis of the disease and effects of coenzyme Q(10) treatment. *Blood*, 119: 5859-5870.
- Pierpoint WS, 2000. Why do plants make medicines? *Biochemist*, 22: 37-40.
- Pietta PG, 2000. Flavonoids as antioxidants. *Journal of Natural Products*. 63: 1035-1042.
- Ravindran KC, Indrajith A, Balakrishnan V, Venkatesan K, Kulandaivelu G (2010) Determination of defense mechanism in *Phaseolus trilobus* Ait seedlings treated under UV-B radiation. *African Crop Science Journal*, 16:111-118.
- Reddy KJ, Kakani VG, Zhao D, Mohammed AR, Gao W, 2003. Cotton responses to ultraviolet-B radiation: experimentation and algorithm development. *Agricultural and Forest Meteorology*, 120: 249-265.
- Romanova AS, Patudin AV, Bankovskii AI, 1978. Quinones of higher plants as possible therapeutic agents. *Khimiko-Farmatsevticheskii Zhurnal*, 11: 53-65.
- Rozema J, van de Staaij J, Björn LO, Caldwell MM, 1997. UV-B as an environmental factor in plant life: stress and regulation. *Trends in Ecology & Evolution*, 12: 22-28.
- Runeckles VC, Krupa SV, 1994. The impact of UV-B radiation and ozone on terrestrial vegetation. *Environmental Pollution*, 83: 191-213.
- Scalbert A., Manach C, Morand C, Remesy C., Jiménez L, 2005. Dietary polyphenols and the prevention of diseases. *Critical Reviews in Food Science and Nutrition*, 45: 287-306.
- Schirmacher G, Schnitzler WH, Grassmann J, 2004. Determination of secondary metabolites and antioxidative capacity as new parameters for quality evaluation – indicated by the new Asia salad *Gynura bicolor*. *Journal of Applied Botany and Food Quality*, 78: 133-134.
- Schmidt S, Zeitz M, Schreiner M, Rohn S, Kroh LW, Krumbein A, 2011. Influence of UV-B on flavonol aglycones and main flavonol glycosides in kale (*Brassica oleracea* var. *sabellica*). In: *Proceedings UV4growth, COST Action FA0906, 7–9 February, Szeged, Hungary*, p. 27.
- Schreiner M, 2009. Die Rolle des Verbrauchers in der Wertschöpfungskette. In: *Status quo und Perspektiven des deutschen Gartenbaus*, Dirksmeyer W (Ed.), *Landbauforschung vti, Sonderheft 330, Braunschweig, Germany*, pp. 99-109.
- Schreiner M, Huyskens-Keil S, 2006. Phytochemicals in fruit and vegetables: health promotion and postharvest elicitors. *Critical Reviews in Plant Sciences*, 25: 267-278.
- Schreiner M, Krumbein A, Knorr D, Smetanska I, 2011. Enhancing glucosinolates in root exudates of *Brassica rapa* ssp. *rapa* mediated by salicylic acid and methyl jasmonate. *Journal of Agricultural and Food Chemistry*, 59: 1400-1405.
- Schreiner M, Krumbein A, Mewis I, Ulrichs C, Huyskens-Keil S, 2009. Short-term and moderate UV-B radiation effects on secondary plant metabolism in different organs of nasturtium (*Tropaeolum majus* L). *Innovative Food Science and Emerging Technologies*, 10: 93-96.
- Shankar S, Singh G, Srivastava RK, 2007. Chemoprevention by resveratrol: Molecular mechanisms and therapeutic potential. *Frontiers in Bioscience*, 12: 4839-4854.

- Sharma DK, 2006. Pharmacological properties of flavonoids including flavonolignans – Integration of petrocrops with drug development from plants. *Journal of Scientific and Industrial research*, 65: 477-484.
- Singh S, Kumari R, Agrawal M, Agrawal SB, 2012. Differential response of radish plants to supplemental ultraviolet-B radiation under varying NPK levels: chlorophyll fluorescence, gas exchange and antioxidants. *Physiologia Plantarum*, 145: 474-484.
- Skulachev VP, Anisimov VN, Antonenko YN, Bakeeva LE, Chernyak BV, Elichev VP, Filenko OF, Kalinina NI, Kapelko VI, Kolosova NG, Kopnin BP, Korshunova GA, Lichinitser MR, Obukhova LA, Pasyukova EG, Pisarenko OI, Roginsky VA, Ruuge EK, Senin II, Severina II, Skulachev MV, Spivak IM, Tashlitsky VN, Tkachuk VA, Vysokikh MY, Yaguzhinsky LS, Zorov DB, 2009. An attempt to prevent senescence: a mitochondrial approach. *Biochimica et Biophysica Acta (BBA) – Bioenergetics*, 1787: 437-461.
- Son TG, Camandola S, Mattson MP, 2008. Hormetic dietary phytochemicals. *Neuromolecular Medicine*, 10: 236-246.
- Strid A, Chow WS, Anderson JM, 1994. UV-B damage and protection at the molecular level in plants. *Photosynthesis Research*, 39: 475–489.
- Strid A, Porra RJ, 1992. Alterations in pigment content in leaves of *Pisum sativum* after exposure to supplementary UV-B. *Plant Cell Physiology*, 33: 1015–1023.
- Surveswaran S, Cai YZ, Corke H, Sun M, 2007. Systematic evaluation of natural phenolic antioxidants from 133 Indian medicinal plants. *Food Chemistry*, 102: 938-953.
- Tamilselvam K, Braidy N, Manivasagam T, Essa MM, Prasad NR, Karthikeyan S, Thenmozhi AJ, Selvaraju S, Guillemin GJ, 2013. Neuroprotective effects of hesperidin, a plant flavanone, on rotenone-induced oxidative stress and apoptosis in a cellular model for Parkinson's Disease. <http://dx.doi.org/10.1155/2013/102741>.
- Taylor RM, Nikaido O, Jordan BR, Rosamond J, Bray CM, Tobin AK, 1996. Ultraviolet-B induced DNA lesions and their removal in wheat (*Triticum aestivum* L.) leaves. *Plant Cell and Environment*, 19: 171-181.
- Tegelberg R, Julkunen-Tiitto R, Aphalo PJ, 2001. The effects of long-term elevated UV-B on the growth and phenolics of field-grown silver birch (*Betula pendula*). *Global Change Biology*, 7: 839-848.
- Teramura AH, 1983. Effects of ultraviolet-B radiation on the growth and yield of crop plants. *Physiologia Plantarum*, 58: 415-427.
- Tomas-Barberan F, Espin JC, 2001. Phenolic compounds and related enzymes as determinants of quality of fruits and vegetables. *Journal of the Science of Food and Agriculture*, 81: 853-876.
- Treutter D, 2005. Significance of flavonoids in plant resistance and enhancement of their biosynthesis. *Plant Biology*, 7: 581-591.
- Tripathi R, Agrawal SB, 2013. Evaluation of changes in lipid peroxidation, ROS production, surface structures, secondary metabolites, and yield of linseed (*Linum usitatissimum*) under individual and combined stress of ultraviolet-B and ozone using open top chambers. *Indian Journal of Biochemistry and Biophysics*, 50: 318-325.
- Ubi BE, Honda C, Bessho H, Kondo S, Wada M, Kobayashi S, Moriguchi T, 2006. Expression analysis of anthocyanin biosynthetic genes in apple skin: effect of UV-B and temperature. *Plant Science*, 170: 571-578.

- Watzl B, Leitzmann C, 2005. Bioaktive Substanzen in Lebensmitteln. Hippokrates Verlag, Stuttgart, Germany.
- Weston E, Thorogood K, Vinti G, Lopez-Juez E, 2000. Light quantity controls leaf-cell and chloroplast development in *Arabidopsis thaliana* wild type and blue-light-perception mutants. *Planta*, 211: 807–815.
- Wilson KE, Wilson MI, Greenberg BM, 1998. Identification of the flavonoid glycosides that accumulate in response to ultraviolet-B radiation. *Photochemistry and Photobiology*, 67:547-553.
- Wilson MI, Greenberg BM, 1993. Protection of the D1 photosystem II reaction center protein from degradation in ultraviolet radiation following adaptation of *Brassicacnapus* L. to growth in ultraviolet-B. *Photochemistry and Photobiology*, 57: 556–563.
- Yamasaki S, Noguchi N, Mimaki K, 2007. Continuous UV-B irradiation induces morphological changes and the accumulation of polyphenolic compounds on the surface of cucumber cotyledons. *Journal of Radiation Research*, 48: 443-454.
- Youdim K, McDonald J, Kalt W, Joseph J, 2002. Potential role of dietary flavonoids in reducing microvascular endothelium vulnerability to oxidative and inflammatory insults. *The Journal of Nutritional Biochemistry*, 13: 282-288.
- Zangerl AR, Berenbaum MR, 1987. Furanocoumarins in wild parsnip: effects of photosynthetically active radiation, ultraviolet light and nutrition. *Ecology* 68: 516-520.
- Zhang WJ, Björn LO, 2009. The effect of ultraviolet radiation on the accumulation of medicinal compounds in plants. *Fitoterapia*, 80: 207-218.
- Zuk-Golaszewska K, Upadhyaya MK, Golaszewski J, 2003. The effect of UV-B radiation on plant growth and development. *Plant, Soil, and Environment*, 49: 135-140.
- Zykova TA, Zhu F, Zhai X, Ma WY, Ermakova SP, Lee KW, Bode AM, Dong Z, 2008. Resveratrol directly targets COX-2 to inhibit carcinogenesis. *Molecular Carcinogenesis*, 47: 797-805.