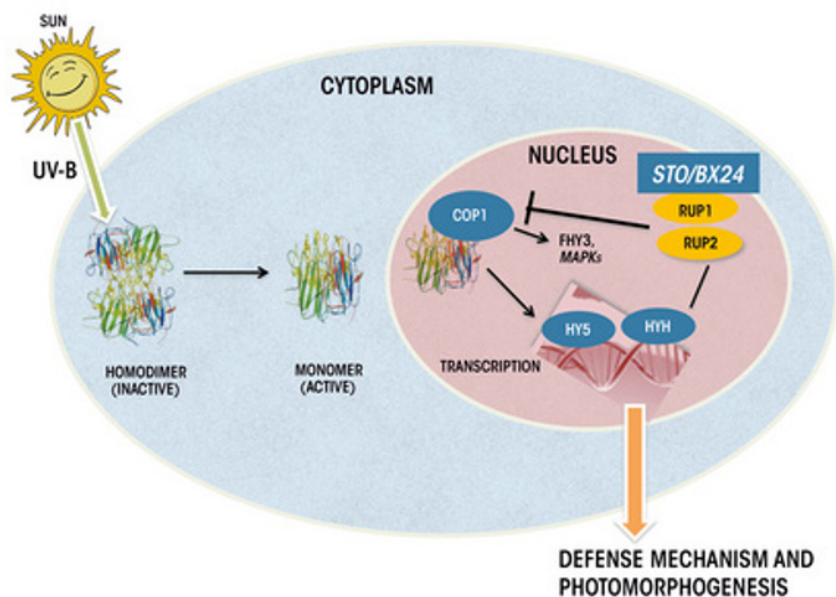


UV-B RADIATION

From Environmental Stressor
to Regulator of Plant Growth



Edited by Vijay Pratap Singh, Samiksha Singh
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WILEY Blackwell

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Founder of Education System in Korea State, India*

Contents

List of Contributors	<i>xv</i>
Preface	<i>xix</i>
1 An Introduction to UV-B Research in Plant Science	1
<i>Rachana Singh, Parul Parihar, Samiksha Singh, MPVVB Singh, Vijay Pratap Singh and Sheo Mohan Prasad</i>	
1.1 The Historical Background	1
1.2 Biologically Effective Irradiance	2
1.3 UV-B-induced Effects in Plants	3
1.4 Conclusion and Future Perspectives	5
Acknowledgements	6
References	6
2 Stimulation of Various Phenolics in Plants Under Ambient UV-B Radiation	9
<i>Marija Vidović, Filis Morina and Sonja Veljović Jovanović</i>	
2.1 Introduction	9
2.2 UV-B Radiation	10
2.3 Phenolics	12
2.3.1 Chemistry of Phenolic Compounds	13
2.3.2 Biosynthesis and Subcellular Localization of Phenolics	13
2.3.3 Functions of Phenolic Compounds Depend on Their Localization	15
2.4 UV-B Radiation Stimulates Phenolic Induction	18
2.4.1 Mechanisms of UV-B Perception	18
2.4.2 UV-B-Induced Accumulation of Phenolic Compounds	20
2.4.3 Interactive Effects of UV-B with UV-A Radiation and PAR on Phenolics Accumulation	29
2.4.4 Interactive Effects of UV-B Radiation with other Environmental Factors on Phenolics Accumulation	30
2.5 UV-B-Induced Photomorphological Responses	31
2.5.1 Connection Between UV-B-Induced Morphological Responses and Phenolics	32
2.5.2 Effect of UV-B Radiation on Root Morphology in Relation to Phenolics	33
2.6 Photosynthesis Under UV-B Radiation	33
2.6.1 Interplay of Phenolics and Photosynthesis Under UV-B Radiation	34

2.7	UV-B Radiation Induces Phenolics Accumulation in Fruits	37
2.8	Conclusion and Future Perspectives	38
	References	39
3	UV-B Radiation: A Reassessment of its Impact on Plants and Crops	57
	<i>Krystyna Żuk-Golaszewska</i>	
3.1	Introduction	57
3.2	Plant Production	58
3.3	Plant Protection Against UV-B	60
	References	60
4	Interaction of UV-B with the Terrestrial Ecosystem	65
	<i>Rohit Kumar Mishra, Sanjesh Tiwari and Sheo Mohan Prasad</i>	
4.1	Introduction	65
4.2	Growth and Development	66
4.3	Secondary Metabolites	67
4.4	Susceptibility to Herbivorous Insects	67
4.5	Plant Sexual Reproduction	67
4.6	Genomic Level	68
4.7	Conclusion	69
	References	70
5	A Review on Responses of Plants to UV-B Radiation Related Stress	75
	<i>Sonika Sharma, Soumya Chatterjee, Sunita Kataria, Juhie Joshi, Sibnarayan Datta, Mohan G Vairale and Vijay Veer</i>	
5.1	Introduction	75
5.2	Morphological and Yield Response to UV-B	76
5.3	Targets of UV-B in the Carbon Fixation Cycle	79
5.4	Photoreceptors and Signalling Pathway in Response to UV-B Radiation	80
5.5	Acclimatization and Protection in Response to UV-B	82
5.6	Oxidative Stress and Antioxidant System in Response to UV-B	82
5.7	DNA Damage and Repair Mechanism	83
5.8	Exclusion of UV Components: Experimental Approach to Study the Effect on Plants	85
5.9	Conclusion and Future Perspectives	86
	Acknowledgement	87
	References	87
6	Oxidative Stress and Antioxidative Defence System in Plants in Response to UV-B Stress	99
	<i>Sunita Kataria</i>	
6.1	Introduction	99
6.2	Plant Protection Against UV Radiation	101
6.3	UV-B and ROS	103
6.4	UV-B and Antioxidant Enzymes	104
6.5	UV-B and Antioxidant	107
6.6	UV-B and Signalling	108
6.7	Conclusion and Future Perspectives	110
	References	111

7	Major Influence on Phytochrome and Photosynthetic Machinery Under UV-B Exposure	123
	<i>Anita Singh, Gausiya Bashri and Sheo Mohan Prasad</i>	
7.1	Introduction	123
7.2	Photomorphogenesis in Higher Plants	124
7.2.1	Phytochrome System and its Interaction with UV-B	124
7.2.2	Photomorphogenic Responses of UV-B	125
7.2.3	UV-B Signal Transduction (UVR8)	127
7.3	Effect of UV-B Exposure on Photosynthetic Machinery	128
7.3.1	Direct Effects of UV- B on Photosynthetic Machinery	128
7.3.1.1	Effects of UV-B Stress on Components Involved in Light Reaction	128
7.3.1.2	Effect of UV-B Stress on Photosystems and Cytochrome b6/f Complex	129
7.3.2	Indirect Effect of UV-B Stress on Components Involved in Dark Reaction	132
7.3.2.1	Impact on Regulation of Stomata and Rubisco Enzyme	132
7.3.3	UV-B induced ROS Production in Plants	133
7.3.4	Protective Adaptation	133
7.4	Conclusion and Future Perspectives	135
	References	136
8	UV-B Radiation-Induced Damage of Photosynthetic Apparatus of Green Leaves: Protective Strategies vis-a-vis Visible and/or UV-A Light	143
	<i>Padmanava Joshi</i>	
8.1	Introduction	143
8.2	UV-B Effects on the Photosynthetic Apparatus of Leaves	143
8.3	UV-A Effects on Photosynthetic Apparatus of Leaves (Damage and Promotion)	145
8.4	UV-A-Mediated Modulation of UV-B-Induced Damage	145
8.5	PAR-Mediated Balancing of UV-B-Induced Damage	146
8.6	Photosynthetic Adaptation and Acclimation to UV-B Radiation	146
8.7	Corroboration with Sensible Approach	147
8.8	Conclusion	149
	Acknowledgements	149
	References	149
9	Ultraviolet Radiation Targets in the Cellular System: Current Status and Future Directions	155
	<i>Parul Parihar, Rachana Singh, Samiksha Singh, MPVVB Singh, Vijay Pratap Singh and Sheo Mohan Prasad</i>	
9.1	Introduction	155
9.2	Absorption Characteristics of Biomolecules	156
9.3	Action Spectrum	156
9.4	Targets of UV-B	157
9.4.1	Interaction with Nucleic acids	157
9.4.1.1	Deoxyribonucleic Acids	158
9.4.1.2	Ribonucleic Acids	159

9.4.2	Proteins	159
9.4.2.1	Tryptophan (Trp)	160
9.4.2.2	Tyrosine (Tyr)	160
9.4.2.3	Phenylalanine (Phe)	162
9.4.2.4	Histidine (His)	162
9.5	The Photosynthetic Machinery	163
9.5.1	Photosystem I and II	164
9.5.2	The Light-Harvesting Complexes	165
9.6	Cell Division and Expansion	167
9.7	Conclusion and Future Perspectives	168
	Acknowledgements	169
	References	169

10 Silicon: A Potential Element to Combat Adverse Impact of UV-B in Plants 175

Durgesh Kumar Tripathi, Shweta, Shweta Singh, Vaishali Yadav, Namira Arif, Swati Singh, Nawal Kishor Dubey and Devendra Kumar Chauhan

10.1	Introduction	175
10.2	The Role of Silicon Against UV-B Exposure on Morphology of Plants	178
10.3	The Defensive Role of Silicon Against UV-B Exposure on Physiological and Biochemical Traits of Plants	179
10.4	Silicon Repairs Anatomical Structures of Plants Damaged by UV-B Exposures	180
10.5	UV-B-induced Oxidative Stress and Silicon Supplementation in Plants	181
10.6	Silicon Supplementation and the Status of Antioxidant Enzymes in Plants Exposed to UV-B	183
10.7	Silicon and Level of Phenolic Compounds Under UV-B Stress	184
10.8	Conclusion and Future Perspectives	186
	References	187

11 Sun-Screening Biomolecules in Microalgae: Role in UV-Photoprotection 197

Rajesh P Rastogi, Ravi R Sonani, Aran Incharoensakdi and Datta Madamwar

11.1	Introduction	197
11.2	Global Climate Change and UV Radiation	198
11.3	Effects of UV Radiation on Microalgae	199
11.4	UV-induced Defence Mechanisms	201
11.5	Sun-Screening Biomolecules as Key UV Photoprotectants	201
11.5.1	Mycosporine-Like Amino Acids (MAAs)	202
11.5.2	Scytonemin	204
11.6	UV-Induced Biosynthesis	206
11.7	Photoprotective Function	207
11.8	Conclusion	208
	Acknowledgements	208
	References	208

12	Plant Response: UV-B Avoidance Mechanisms	217
	<i>Sunil K Gupta, Marisha Sharma, Farah Deeba and Vivek Pandey</i>	
12.1	Introduction	217
12.2	Ultraviolet Radiation: Common Source, Classification and Factors	219
12.2.1	Common Sources of UVR	219
12.2.2	Classification	219
12.2.3	Environmental Factors Affecting UV Level	220
12.3	UV-B and Human Health	220
12.3.1	Effects on the Skin	220
12.3.2	Effects on the Eyes	220
12.4	UV-B and Plant Responses	220
12.4.1	Morphological Responses	220
12.4.1.1	Visible Symptoms	220
12.4.1.2	Plant Growth and Leaf Phenology	221
12.4.1.3	Reproductive Morphology	222
12.4.1.4	UV-B-induced photomorphogenesis	222
12.4.2	Leaf Ultrastructure and Anatomy	222
12.4.3	Crop Yield	223
12.4.4	Photosynthesis	225
12.4.4.1	Pigments	225
12.4.4.2	Photosynthetic Machinery	225
12.4.5	Biochemical Responses	226
12.4.5.1	ROS Production in Plants	226
12.4.5.2	Free Radical Scavenging Mechanism	227
12.4.6	Molecular Responses	227
12.4.6.1	UV-B and Genes	227
12.4.6.1.1	Genes Damaged by UV Radiation	228
12.4.6.1.2	DNA Damage	228
12.4.6.2	UV and Proteins	230
12.4.6.2.1	Amino acids	231
12.5	UV-B Avoidance and Defence Mechanism	234
12.5.1	Avoidance at Morphological Level	234
12.5.1.1	Epicuticular Waxes	234
12.5.2	Avoidance at Biochemical Level	235
12.5.2.1	Possible Role of Pectin Endocytosis in UV-B Avoidance	235
12.5.3	Avoidance at the Molecular Level	236
12.5.3.1	DNA Repair	236
12.5.3.2	Genes and Avoidance	237
12.5.3.3	UV-B perceived by UVR8 Strongly Inhibits Shade Avoidance	237
12.5.4	UV-B and Secondary Metabolites	238
12.5.4.1	Plant Phenolics	238
12.5.4.2	Anthocyanin	239
12.5.4.3	Alkaloids	240
12.5.4.4	Isoprenoids	240
12.5.4.5	Glucosinolates	240
12.6	UV-B and its Significance	240
12.6.1	Ecological Significance	240
12.6.2	UV-B and Plant Competition	241

12.7 Conclusion and Future Perspectives 242

Acknowledgments 243

References 244

13 Impact of UV-B Exposure on Phytochrome and Photosynthetic Machinery: From Cyanobacteria to Plants 259

Shivam Yadav, Alok Kumar Shrivastava, Chhavi Agrawal, Sonia Sen, Antra Chatterjee, Shweta Rai, Ruchi Rai, Shilpi Singh and LC Rai

13.1 Introduction 259

13.2 Effect of UV-B Irradiation on Photosynthetic Machinery of Cyanobacteria 260

13.2.1 Pigments 260

13.2.2 Photosynthetic Electron Transport System 261

13.2.3 Photophosphorylation and CO₂ Fixation 262

13.3 Effect of UV-B Irradiation on Photosynthetic Machinery of Algae 262

13.4 Effect of UV-B Irradiation on Photosynthetic Machinery of Higher Plants 264

13.4.1 Pigments 264

13.4.1.1 Phytochrome 264

13.4.1.2 Chlorophylls, Carotenoids and Other Pigments 265

13.4.2 Photosystem II 265

13.4.2.1 Oxygen-evolving Complex 266

13.4.2.2 Plastoquinones and Redox-active Tyrosines 266

13.4.2.3 D1 and D2 Proteins 267

13.4.3 Photosystem I 267

13.4.4 Cytochrome b6/f Complex, ATP Synthase and Rubisco 267

13.4.5 Net Photosynthesis 268

13.5 Conclusion and Future Perspectives 268

Acknowledgements 268

References 269

14 Discovery of UVR8: New Insight in UV-B Research 279

Shivam Yadav and Neelam Atri

14.1 Introduction 279

14.2 Photoperception in Plants 280

14.3 Discovery of UVR8: UV-B Photoreceptor 280

14.4 UVR8 Structure 281

14.4.1 Salt Bridge Interactions Mediate UVR8 Dimerization 281

14.4.2 Chromophore and Key Tryptophan Residues 281

14.5 Physiological Roles of UVR8 283

14.5.1 Photomorphogenic Response Regulation by UVR8 283

14.5.2 Regulation of Flavonoid Biosynthesis 284

14.5.3 Plant-Pathogen and Plant-Herbivore Interactions 284

14.6 Conclusion and Future Perspectives 284

References 285

15	UVR8 Signalling, Mechanism and Integration with other Pathways	289
	<i>Antra Chatterjee, Alok Kumar Shrivastava, Sonia Sen, Shweta Rai, Shivam Yadav, Ruchi Rai, Shilpi Singh and LC Rai</i>	
15.1	Introduction	289
15.2	UVR8-Arbitrated Signalling	290
15.2.1	Constitutively Photomorphogenic 1 (COP1)	290
15.2.2	Elongated Hypocotyl 5 (HY5) and HYH	291
15.2.3	Repressor of UV-B Photomorphogenesis 1 (RUP1)and RUP2	292
15.3	Molecular Mechanism of Photoreceptor-Mediated Signalling	293
15.4	UVR8 Involvements in Different Pathways	296
15.4.1	Protection from Photo-Inhibition and Photo Oxidative Stress	297
15.4.2	Flavonoid and Alkaloid Pathways	298
15.4.3	DNA Damage Repair	299
15.4.4	Defence Against Pathogens	299
15.4.5	Inhibition of Plant Shade Avoidance	300
15.4.6	Regulation of Leaf Morphogenesis	300
15.4.7	Regulation of Root Growth and Development	300
15.4.8	Circadian Clock	301
15.5	Conclusion and Future Perspectives	301
	Acknowledgements	302
	References	302

Index	309
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Preface

In the course of acquiring knowledge about UV-B research in plant systems from the past up to the present day, we have found a considerable gap between the availability of books and emerging areas of research. This book has been written to bridge the gap between researches being conducted from the past up to today, and the direction these researches might take in the future with respect to UV-B.

The title itself indicates that this book has mapped UV-B research from past up to recent times. It is a book of theoretical knowledge, and the compilation has been done on the basis of practical work done by the researchers and scientists. We have briefed out the historical backgrounds of UV-B namely, how it reaches the earth's surface, its action spectra and its interaction with living systems, using the research work conducted by researchers in the past, to recent studies that show how research in UV-B has taken a U-turn with the discovery of UVR8.

A good book is one that includes knowledge for all readers, including students, and of course we are indebted to the many authors who have contributed to it. This book includes chapters which cover several aspects of UV-B, starting from the basics of UV-B research and going on to the present date, and a brief outline has been provided below.

The first chapter gives an overview of the ozone layer and the reasons for its depletion and UV-B reaching the earth's surface, and it also offers a brief introduction to action spectra and biologically effective irradiance. In later sections, the authors also discuss the impact of UV-B on plants by analysing the researches performed in the past.

The second chapter gives a brief historical background for the effect of ambient UV-B on plants, with special reference to accumulation of secondary metabolites, such as phenolic compounds, alkaloids and terpenoids. The authors have also discussed recent studies regarding phenolics under ecologically relevant UV-B radiation, and changes in the content of secondary metabolites, with reference to species variation, changes in the UV-B : UV-A : PAR ratio, UV-B doses and UV-B spectral quality.

In the next few chapters, authors discuss risk arising due to the interaction of UV-B with the components of plants, and biological effects arising due to absorption of UV radiation, whether from UV-A or UV-B, by important biomolecules like nucleic acids, lipids and proteins. They also examine the impact on the phytochrome system and photosynthetic machinery. In addition, the authors also discuss the effects of UV-B radiation in terms of oxidative stress, and the responses generated by plants to combat from the stress arising due to UV-B induced toxicity, which includes accumulation of sun-screen molecules. These chapters basically focus on the past researches that have been performed with UV-B. With technology and research advancement,

the introduction of photomorphogenic responses came into existence, which compelled researchers to gain a deeper insight into this phenomenon, and this curiosity for innovation led to the discovery of UVR8.

In later chapters, authors have very well documented the history of photomorphogenic responses and how UVR8 was discovered – and all the regulators, whether positive or negative, involved with this component. In the last chapter, the authors discuss the mechanism of regulatory action by UVR8 and its integration with other pathways.

In concluding, it is a pleasure to express our thanks to all the authors for contributing chapters that have helped us in giving a clear picture of the changing scenario of research in UV-B. We hope that this book will be of special value to environmentalists, researchers and students seeking knowledge on UV-B, which has not yet been assimilated in textbooks.

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An Introduction to UV-B Research in Plant Science

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1.1 The Historical Background

About 3.8×10^9 years ago, during the early evolutionary phase, the young earth was receiving a very high amount of UV radiation and it is estimated that, at that time, the sun was behaving like young T-Tauristars and was emitting 10,000 times greater UV than today (Canuto *et al.*, 1982). Then, the radiance of the sun became lower than it is in the present day, thereby resulting in temperatures below freezing. On the other hand, due to high atmospheric carbon dioxide (CO₂) level, which was 100–1000 times greater than that of present values, liquid water did occur and absorbed infrared (IR) radiation, and this shaped an obvious greenhouse effect (Canuto *et al.*, 1982). Due to the photosynthesis of photosynthetic bacteria, cyanobacteria and eukaryotic algae, oxygen (O₂) was released for the first time into the environment, which led to an increase of atmospheric O₂ and a simultaneous decrease of atmospheric CO₂.

About 2.7×10^9 years ago, due to the absence of oxygenic photosynthesis, oxygen was absent from the atmosphere. About 2.7×10^9 years ago, with the deposition of iron oxide (Fe₂O₃) in Red Beds, aerobic terrestrial weathering occurred and, at that time, O₂ was approximately about 0.001% of the present level (Rozema *et al.*, 1997). In proportion with gradual atmospheric O₂ increase, the accumulation of stratospheric ozone might have been slow. Alternatively, about 3.5×10^8 years ago, due to a sheer rise in atmospheric oxygen, it might have reached close to the present levels of 21% (Kubitzki, 1987; Stafford, 1991). Nevertheless, terrestrial plant life was made possible by the development of the stratospheric ozone (O₃) layer, which absorbs solar UV-C completely and a part of UV-B radiation, thereby reducing the damaging solar UV flux on the earth's surface (Caldwell, 1997).

Before focusing on the various aspects of UV-B radiation, we should firstly understand the electromagnetic spectrum. The electromagnetic spectrum consists of ultraviolet

Table 1.1 Regions of the electromagnetic spectrum together with colours, modified from Iqbal (1983) and Eichler *et al.* (1993).

Wavelength (nm)	Frequency (THz)	Colour
50 000–10 ⁶	6–0.3	far IR
3000–50 000	100–6	mid IR
770–3000	390–100	near IR
622–770	482–390	red
597–622	502–482	Orange
577–597	520–502	yellow
492–577	610–520	Green
455–492	660–610	blue
390–455	770–660	violet
315–400	950–750	UV-A
280–315	1070–950	UV-B
100–280	3000–1070	UV-C

(UV) and visible (VIS) radiations (i.e. also PAR). The wavelength ranges of UV and visible radiation are listed in Table 1.1. Solar radiations, with a longer wavelength, are called infrared (IR) radiations. The spectral range between 200 and 400 nm, which borders on the visible range, is called UV radiation, and is divided into three categories: UV-C (100–280 nm), UV-B (280–315 nm) and UV-A (315–400 nm). The shorter wavelengths of UV get filtered out by stratospheric O₃, and less than 7% of the sun's radiation range between 280 and 400 nm (UV-A and UV-B) reaches the Earth's surface.

The level of UV-B radiation over temperate regions is lower than it is in tropical latitudes, due to higher atmospheric UV-B absorption, primarily caused by changes in solar angle and the thickness of the ozone layer. Therefore, the intensity of UV-B radiation is relatively low in the polar regions and high in the tropical areas. Over 35 years ago, it was warned that man-made compounds (e.g. CFCs, HCFCs, halons, carbon tetrachloride, etc.) cause the breakdown of large amounts of O₃ in the stratosphere (Velders *et al.*, 2007) thereby increasing the level of UV-B reaching the Earth's surface. Increase in the UV-B radiation has been estimated since the 1980s (UNEP, 2002), and projections like the Kyoto protocol estimate that, even after the implementation of these protocols, returning to pre-1980 levels will be possible by 2050–2075 (UNEP, 2002).

1.2 Biologically Effective Irradiance

The term 'biologically effective irradiance' means the effectiveness of different wavelengths in obtaining a number of photobiological outcomes when biological species are irradiated with ultraviolet radiations (UVR). The UV-B, UV-A and photosynthetically active radiations (PAR; 400–700 nm) have a significant biological impact on organisms (Vincent and Roy, 1993; Ivanov *et al.*, 2000). Ultraviolet irradiation results into a

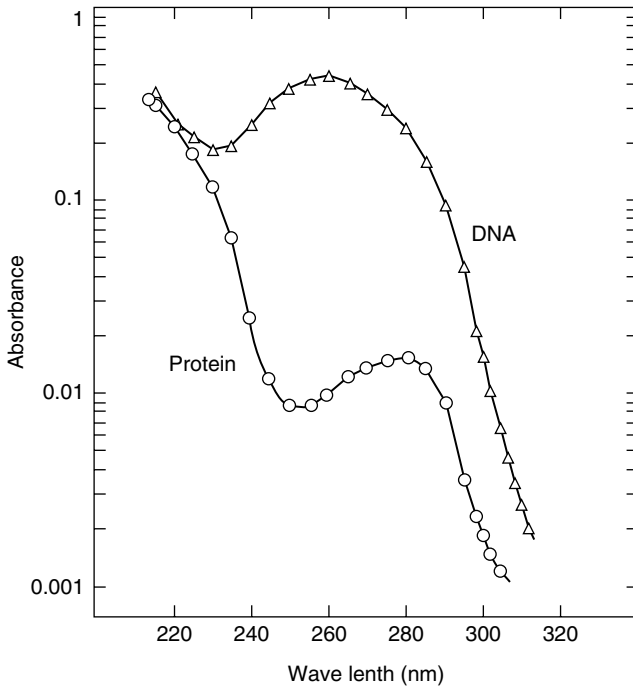


Figure 1.1 Absorption spectra of protein and DNA at equal concentrations (adapted from Harm, 1980).

number of biological effects that are initiated by photochemical absorption by biologically significant molecules. Among these molecules, the most important are nucleic acids, which absorb the majority of ultraviolet photons, and also proteins, which do so to a much lesser extent (Harm, 1980).

Nucleic acids (a necessary part of DNA) are nucleotide bases that have absorbing centres (i.e. chromophores). In DNA, the absorption spectra of purine (adenine and guanine) and pyrimidine derivatives (thymine and cytosine), are slightly different, but an absorption maximum between 260–265 nm, with a fast reduction in the absorption at longer wavelengths, is common (Figure 1.1). In contrast with nucleic acids solutions of equal concentration, the absorbance of proteins is lower. Proteins with absorption maxima of about 280nm most strongly absorb in the UV-B and UV-C regions (Figure 1.1). The other biologically significant molecules that absorb UVR are carotenoids, porphyrins, quinones and steroids.

1.3 UV-B-induced Effects in Plants

In the past few decades, a lot of studies have been made on the role of UV-B radiation. Due to the fact that sunlight is necessary for their survival, plants are inevitably exposed to solar UV-B radiation reaching the earth's surface. From the point of view of ozone depletion, this UV-B radiation should be considered as an environmental stressor for photosynthetic organisms (Caldwell *et al.*, 2007). However, according to the evolutionary point of view, this assumption is questionable.

Although UV-B radiation comprises only a small part of the electromagnetic spectrum, the UV-B reaching on earth's surface is capable of producing several responses at molecular, cellular and whole-organism level in plants (Jenkins, 2009). UV-B radiation is readily absorbed by nucleic acids, lipids and proteins, thereby leading to their photo-oxidation and resulting in promotional changes on multiple biological processes, either by regulating or damaging (Tian and Yu, 2009). In spite of the multiplicity of UV-B targets in plants, it appears that the main action target of UV-B is photosynthetic apparatus, leading to the impairment of the photosynthetic function (Lidon *et al.*, 2012). If we talk about the negative impact of UV-B, it inhibits chlorophyll biosynthesis, inactivates light harvesting complex II (LHCII), photosystem II (PSII) reaction centres functioning, as well as electron flux (Lidon *et al.*, 2012).

The photosynthetic pathway responding to UV-B may depend on various factors, including UV-B dosage, growth stage and conditions, and flow rate, and also the interaction with other environmental stresses (e.g., cold, high light, drought, temperature, heavy metals, etc.) (Jenkins, 2009). The thylakoid membrane and oxygen evolving complex (OEC) are highly sensitive to UV-B (Lidon *et al.*, 2012). Since the Mn cluster of OEC is the most labile element of the electron transport chain, UV-B absorption by the redox components or protein matrix may lead to conformational changes, as well as inactivation of the Mn cluster. The D1 and D2 are the main proteins of PSII reaction centres and the degradation and synthesis of D1 protein is in equilibrium under normal condition in light, however, its degradation rate becomes faster under UV-B exposure thereby, equilibrium gets disturbed (Savitch *et al.*, 2001; Lidon *et al.*, 2012). In the OEC coupled to PSII, during light-driven photosynthetic electron transport, tri-molecular oxygen is produced continuously, which can be converted in the sequential reduction to superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($\bullet OH$) (Apel and Hirt, 2004). Furthermore, PSI and cytochrome b6/f complex are less affected by UV-B radiation in comparison to PSII (Lidon *et al.*, 2012).

Stomatal movement is an important regulatory process that limits the rate of photosynthesis. In *Vicia faba*, high UV-B radiation stimulates either stomatal opening or closing, depending on the metabolic rate (Jansen and van-den-Noort, 2000). However, the stimulated reduction of stomatal conductance can be responsible for CO_2 limitation, as reported in many plants (Zhao *et al.*, 2003; Lidon and Ramalho, 2011), but the reduction in the stomatal conductance has a lesser extent than that of net photosynthetic rate. Additionally, UV-B radiation strongly affects the activity as well as content of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) in plants (Correia *et al.*, 1998; Savitch *et al.*, 2001). Besides this, the intermediate stage of the Calvin cycle (i.e. sedoheptulose 1,7-bisphosphatase), as well as the regeneration of RuBP, was found to be decreased upon exposure to UV-B radiation (Allen *et al.*, 1998).

UV-B radiation has long been perceived as a stressor. Many studies have shown that it impedes photosynthetic activities, damages DNA, proteins and membranes, and impedes plant growth. Oxidative stress has been flagged as a pioneer factor in such UV-B stress responses (Lidon *et al.*, 2012). However, DNA damage, membrane degradation products, and ROS also play a role in mediating UV-B protection, and have done so since the origin of the first plants. Cyanobacteria first evolved on the earth at a time when UV-B levels were at their highest and no ozone layer existed. Under such high UV-B radiation during the early evolution of photosynthetic organisms, they might have coevolved their genetic machinery along with the ambient UV-B level, which might have also helped the

transition to terrestrial life (Rozema *et al.*, 1997). Therefore, it can be assumed that plants' metabolic machinery must have all the compulsory elements for normal coexistence with present UV-B levels, so the solar UV-B radiation reaching the earth should not be considered to be an environmental stressor. Actually, the current ambient UV-B radiation level should be considered as a signal factor which is capable of inducing the expression of genes related to the normal growth and development of plants (Jenkins, 2009).

A conceptual U-turn has been taken place, and UV-B is rarely considered as a damaging factor. There is overpowering evidence that UV-B is an environmental regulator that controls gene expression, cellular and metabolic activities, and also the growth and development (Jenkins, 2009). Under low UV-B fluence rate, the regulatory role of UV-B can be observed, and these effects are mediated by the UV-B-specific UV Resistance Locus 8 (UVR8) photoreceptor, which has opened the door to elucidate the UV-B signalling pathways in plants (Christie *et al.*, 2012; Wu *et al.*, 2012; Singh *et al.*, 2012; Srivastava *et al.*, 2014).

The UVR8 photoreceptor exists as a homodimer that undergoes immediate monomerization following UV-B exposure, and the process is dependent on an intrinsic tryptophan residue (Rizzini *et al.*, 2011). Upon exposure to UV-B, UVR8 accumulates rapidly, and interacts with Constitutively Photomorphogenic 1 (COP1) to initiate the molecular signalling pathway that leads to gene expression changes. UVR8 monomer is redimerized by the action of RUP1 and RUP2, which interrupts the UVR8-COP1 interaction, thereby inactivating the signalling pathway and regenerating the UVR8 homodimer again, ready for UV-B perception. This signalling leads to UVR8 dependent responses, such as UV-B-induced photomorphogenic responses, and also the accumulation of UV-B-absorbing flavonols (Tilbrook *et al.*, 2013). Elongated Hypocotyl 5 (HY5) acts as a downstream effector, and is regulated by the negative feedback pathway.

Favory *et al.* (2009) hypothesized that during UVR8 interaction with COP1, COP1 might have been taken out from phytochrome (red light receptor) and cryptochrome (blue/UV-A light receptor) under UV-B exposure, and this fact was supported by the phenotype of the *COP1* overexpressing line of UVR8. Conversely, Oravecz *et al.* (2006) and Favory *et al.* (2009) have noted that COP1 was excluded by the nucleus upon exposure to visible light, while UV-B exposure results in nuclear accumulation and stabilization of COP1. In addition, being a repressor of photomorphogenesis, COP1 is dependent on SPA protein, which is not a part of the regulatory action by COP1 (Laubinger *et al.*, 2004; Oravecz *et al.*, 2006). Interestingly, SPA and Repressor of Photomorphogenesis (RUP) genes show similarity in their phylogeny while interacting with COP1 (Gruber *et al.*, 2010; Fittinghoff *et al.*, 2006). All these similarities suggest towards the evolution of complex photoreceptor UVR8 from the other photoreceptors, and the role of UVR8 as a signalling molecule.

1.4 Conclusion and Future Perspectives

Over recent years, significant progress has been made in identifying the molecular players, their early mechanisms and signalling pathway in UV-B perception in plants, but there is more we have to do. Several questions remain to be uncovered, regarding the photochemistry, signal transduction and regulatory mechanisms of UVR8, that need to be addressed and, of course, this will open a new horizon in the field of UV-B perception and signalling. Questions that remain to be traced out include: the primary

responses of UVR8 after UV-B perception; whether functioning at the chromatin level exists; sites of UVR8 functioning in the cell; crosstalk of UVR8 pathway with COP1 and visible light photoreceptors along with their signalling; whether UVR8 has evolved from other photoreceptors as a need of environmental changes and is now towards the degrading or evolutionary phase.

Now the stage is set to tackle these questions. No doubt, the answers will pave a new direction and a deep understanding of plant UV-B responses. Of course, the future of UV-B signalling will be more realistic after the preparation of a detailed molecular map of various signalling molecules regarding UV-B.

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