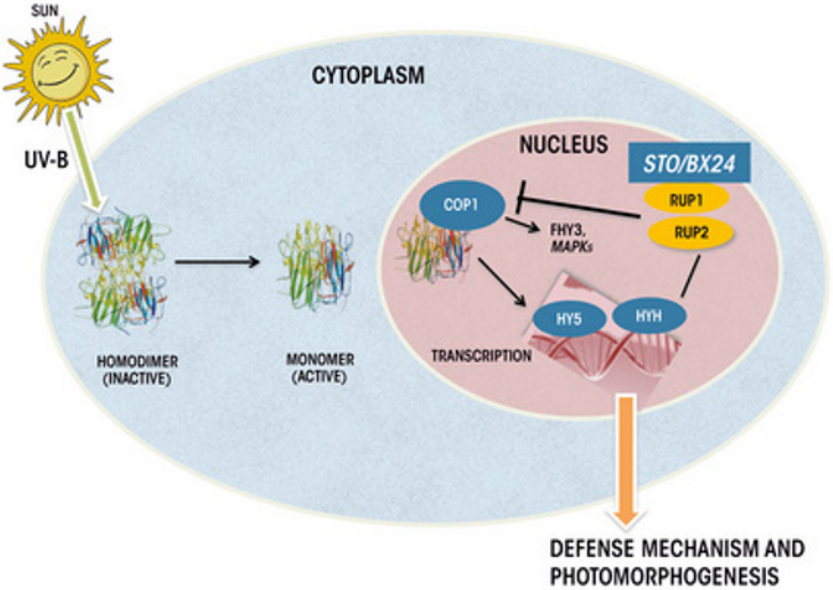
UV-B RADIATION

From Environmental Stressor to Regulator of Plant Growth



Edited by Vijay Pratap Singh, Samiksha Singh
Sheo Mohan Prasad, Parul Parihar

WILEY Blackwell

UV-B Radiation: From Environmental Stressor to Regulator of Plant Growth

UV-B Radiation: From Environmental Stressor to Regulator of Plant Growth

Edited by

Vijay Pratap Singh
Chhattisgarh, India

Samiksha Singh
Allahabad, India

Sheo Mohan Prasad
Allahabad, India

Parul Parihar
Allahabad, India

WILEY Blackwell

This edition first published 2017 © 2017 by John Wiley & Sons Ltd

Registered Office
John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Offices
9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com/wiley-blackwell.

The right of Vijay Pratap Singh, Samiksha Singh, Sheo Mohan Prasad, and Parul Parihar to be identified as the author(s) of the editorial material in this work has been asserted in accordance with the UK Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs and Patents Act 1988, without the prior permission of the publisher.

Designations used by companies to distinguish their products are often claimed as trademarks. All brand names and product names used in this book are trade names, service marks, trademarks or registered trademarks of their respective owners. The publisher is not associated with any product or vendor mentioned in this book.

Limit of Liability/Disclaimer of Warranty: While the publisher and author(s) have used their best efforts in preparing this book, they make no representations or warranties with respect to the accuracy or completeness of the contents of this book and specifically disclaim any implied warranties of merchantability or fitness for a particular purpose. It is sold on the understanding that the publisher is not engaged in rendering professional services and neither the publisher nor the author shall be liable for damages arising herefrom. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

Library of Congress Cataloging-in-Publication data has been applied for.

ISBN: 9781119143604

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover design: Wiley
Cover image: Courtesy of Vijay Pratap Singh, previously published in Journal of Photochemistry & Photobiology, B: Biology 153 (2015) 334–343 © Elsevier.

Set in 10/12pt Warnock by SPi Global, Pondicherry, India

10 9 8 7 6 5 4 3 2 1

Raja Ramanuj Pratap Singhdev (1901–1954)
Founder of Education System in Korea State, India

Contents

15 UVR8 Signalling, Mechanism and Integration with other Pathways 289

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

List of Contributors

Chhavi Agrawal
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Namira Arif
DD Pant Interdisciplinary Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Neelam Atri
MMV, Banaras Hindu University
Varanasi, India

Gausiya Bashri
Ranjan Plant Physiology and
Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Soumya Chatterjee
Defence Research Laboratory, DRDO
Tezpur, Assam, India

Antra Chatterjee
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Devendra Kumar Chauhan
DD Pant Interdisciplinary
Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Sibnarayan Datta
Defence Research Laboratory, DRDO
Tezpur, Assam, India

Farah Deeba
Plant Ecology & Environmental Science
CSIR-National Botanical Research
Institute
Rana Pratap Marg
Lucknow, India

Nawal Kishor Dubey
Center of Advanced Studies
Department of Botany
Banaras Hindu University
Varanasi, India

Sunil K Gupta
Plant Ecology & Environmental
Science
CSIR-National Botanical Research
Institute
Rana Pratap Marg
Lucknow, India

Aran Incharoensakdi
Laboratory of Cyanobacterial Biotechnology
Department of Biochemistry
Faculty of Science
Chulalongkorn University
Bangkok, Thailand

Juhie Joshi
Photobiology Lab
School of Life Sciences
DAVV
Indore, India

Padmanava Joshi
Formerly Reader in Physics-cum-Principal
Anchal College
Padampur, Rajborasambar
Bargarh, Odisha, India

Sonja Veljović Jovanović
Institute for Multidisciplinary Research,
University of Belgrade, Kneza Višeslava,
1, 11000, Belgrade, Serbia

Sunita Kataria
Photobiology Lab
School of Life Sciences
DAVV
Indore, India

Datta Madamwar
BRD School of Biosciences
Vadtal Road, Satellite Campus
Sardar Patel University
Vallabh Vidyanagar, Anand
Gujarat, India

Rohit Kumar Mishra
Ranjan Plant Physiology and
Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Filis Morina
Institute for Multidisciplinary Research
University of Belgrade, Kneza Višeslava,
1, 11000, Belgrade, Serbia

Vivek Pandey
Plant Ecology & Environmental
Science
CSIR-National Botanical Research
Institute
Rana Pratap Marg
Lucknow, India

Parul Parihar
Ranjan Plant Physiology and
Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Sheo Mohan Prasad
Ranjan Plant Physiology and
Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

LC Rai
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Ruchi Rai
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Shweta Rai
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Rajesh P Rastogi
BRD School of Biosciences
Vadtal Road, Satellite Campus
Sardar Patel University
Vallabh Vidyanagar, Anand
Gujarat, India

Sonia Sen
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Marisha Sharma
Plant Ecology & Environmental Science
CSIR-National Botanical Research Institute
Rana Pratap Marg
Lucknow, India

Sonika Sharma
Defence Research Laboratory
DRDO, Tezpur
Assam, India

Alok Kumar Shrivastava
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Anita Singh
Ranjan Plant Physiology and Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

MPVVB Singh
Ranjan Plant Physiology and Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Rachana Singh
Ranjan Plant Physiology and Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Samiksha Singh
Ranjan Plant Physiology and Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Shilpi Singh
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Shweta
DD Pant Interdisciplinary Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Shweta Singh
DD Pant Interdisciplinary Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Swati Singh
DD Pant Interdisciplinary Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Vijay Pratap Singh
Government Ramanuj Pratap Singhdev Post Graduate College
Baikunthpur, Koriya
Chhattisgarh, India

Ravi R Sonani
BRD School of Biosciences
Vadtal Road, Satellite Campus
Sardar Patel University
Vallabh Vidyanagar, Anand
Gujarat, India

Sanjesh Tiwari
Ranjan Plant Physiology and
Biochemistry Laboratory
Department of Botany
University of Allahabad
Allahabad, India

Durgesh Kumar Tripathi
Center of Advanced Studies
Department of Botany
Banaras Hindu University
Varanasi, India

Mohan G Vairale
Defence Research Laboratory, DRDO
Tezpur, Assam, India

Vijay Veer
Defence Research Laboratory, DRDO
Tezpur, Assam, India

Marija Vidović
Institute for Multidisciplinary Research
University of Belgrade
Kneza Višeslava, 1, 11000
Belgrade, Serbia

Vaishali Yadav
DD Pant Interdisciplinary Research Lab
Department of Botany
University of Allahabad
Allahabad, India

Shivam Yadav
Molecular Biology Section
Centre of Advanced Study in Botany
Banaras Hindu University
Varanasi, India

Krystyna Żuk-Gołaszewska
Department of Agrotechnology
Agricultural Production Management
and Agribusiness
University of Warmia and Mazury
in Olsztyn
Poland

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.

Editors:
Vijay Pratap Singh
Samiksha Singh
Sheo Mohan Prasad
Parul Parihar

1

An Introduction to UV-B Research in Plant Science

Rachana Singh[1]*, Parul Parihar*[1]*, Samiksha Singh*[1]*, MPVVB Singh*[1]*,*
Vijay Pratap Singh[2] *and Sheo Mohan Prasad*[1]

[1] *Ranjan Plant Physiology and Biochemistry Laboratory, Department of Botany, University of Allahabad, Allahabad, India*
[2] *Government Ramanuj Pratap Singhdev Post Graduate College, Baikunthpur, Koriya, Chhattisgarh, India*

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 (CO_2) 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 (O_2) was released for the first time into the environment, which led to an increase of atmospheric O_2 and a simultaneous decrease of atmospheric CO_2.

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 (Fe_2O_3) in Red Beds, aerobic terrestrial weathering occurred and, at that time, O_2 was approximately about 0.001% of the present level (Rozema *et al.*, 1997). In proportion with gradual atmospheric O_2 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 (O_3) 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

UV-B Radiation: From Environmental Stressor to Regulator of Plant Growth, First Edition. Edited by
Vijay Pratap Singh, Samiksha Singh, Sheo Mohan Prasad and Parul Parihar.

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 O_3, 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 O_3 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

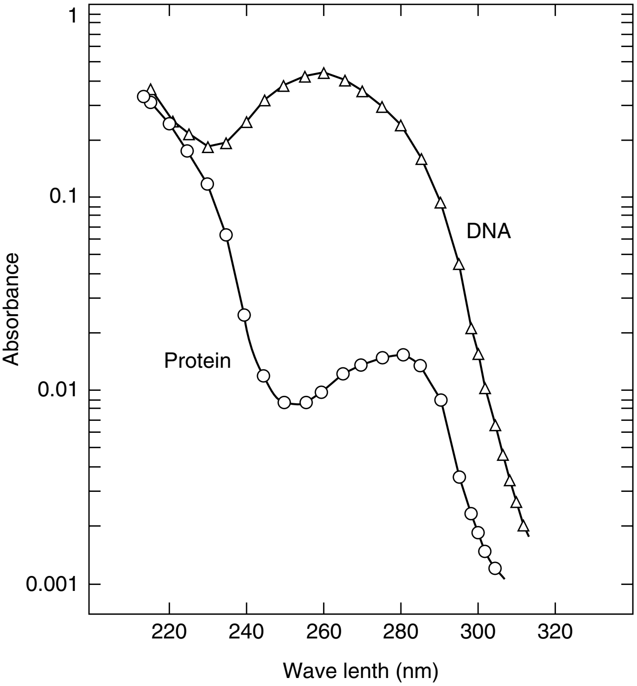


Figure 1.1 Absorption spectra of protein and DNA at equal concentrations (adapted from Harm, 1980).

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 280 nm most strongly absorb in the UV-B and UV-C regions (Figure 1.1). The other biologically significant molecules that absorb UVR are caratenoids, 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 necessity 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.

Acknowledgements

The University Grants Commission, New Delhi is greatly acknowledged for financial support.

References

Allen DJ, Nogués S, Baker NR (1998). Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? *Journal of Experimental Botany* **49**, 1775–1788.

Apel K, Hirt H (2004). Reactive oxygen species: Metabolism, oxidative stress and signal transduction. *Annual Review of Plant Biology* **55**, 373–399.

Caldwell MM (1979). Plant life and ultraviolet radiation: some perspectives in the history of the earth's UV climate. *BioScience* **29**, 520–525.

Caldwell MM, Bornman JF, Ballaré CL, Flint SD, Kulandaivelu G (2007). Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. *Photochemical & Photobiological Sciences* **6**, 252–266.

Canuto VM, Levine JS, Augustsson TR, Imhoff CL (1982). UV radiation from the young sun and oxygen and ozone level in the prebiological palaeoatmosphere. *Nature* **296**, 816–820.

Christie JM, Arvai AS, Baxter KJ, Heilmann M, Pratt AJ, O'Hara A, Kelly SM, Hothorn M, Smith BO, Hitomi K, Jenkins GI, Getzoff ED (2012). Plant UVR8 photoreceptor senses UV-B by tryptophan-mediated disruption of cross-dimer salt bridges. *Science* **335**, 1492–1496.

Correia CM, Areal ELV, Torres-Pereira MS, Torres-Pereira JMG (1998). Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. I. Growth and morphological aspects. *Field Crops Research* **59**(2), 81–89.

Eichler HJ, Fleischner A, Kross J, Krystek M, Lang H, Niedrig H, Rauch H, Schmahl G, Schoenebeck H, Sedlmayr E (1993). Bergmann, Schaefer: *Lehrbuch der Experimentalphysik Band 3*: Optik. Ed. by H. Niedrig. Verlag Walter de Gruyter Berlin/New York (cit. on p. 3).

Favory JJ, Stec A, Gruber H, Rizzini L, Oravecz A, Funk M, Albert A, Cloix C, Jenkins GI, Oakeley EJ, Seidlitz HK, Nagy F, Ulm R (2009). Interaction of COP1 and UVR8 regulates UVB- induced photomorphogenesis and stress acclimation in *Arabidopsis*. *The EMBO Journal* **28**, 591–601.

Fittinghoff K, Laubinger S, Nixdorf M, Fackendahl P, Baumgardt RL, Batschauer A, Hoecker U (2006). Functional and expression analysis of Arabidopsis SPA genes during seedling photomorphogenesis and adult growth. *The Plant Journal* **47**, 577–590.

Gruber H, Heijde M, Heller W, Albert A, Seidlitz HK, Ulm R (2010). Negative feedback regulation of UV-B-induced photomorphogenesis and stress acclimation in *Arabidopsis. Proceedings of the National Academy of Sciences of the United States of America* **107**, 20132–20137.

Harm W (1980). *Biological effects of ultraviolet radiation.* Cambridge: Cambridge University Press.

Iqbal M (1983). *An introduction to solar radiation.* Academic Press Canada (cit. on pp. 3, 8).

Ivanov AG, Miskiewicz E, Clarke AK, Greenberg BM, Huner NPA (2000). Protection of Photosystem I1 against UV-A and UV-B radiation in the cyanobacterium Plectonemu boryanum: the role of growth temperature and growth irradiance. *Photochemistry and Photobiology* **72**, 772–779.

Jansen MAK, van-den-Noort RE (2000). Ultraviolet-B radiation induces complex alterations in stomatal behavior. *Physiologia Plantarum* **110**, 189–194.

Jenkins GI (2009). Signal transduction in responses to UV-B radiation. *Annual Review of Plant Biology* **60**, 407–431.

Kubitzki K (1987). Phenylpropanoid metabolism in land plant evolution. *Journal of Plant Physiology* **131**, 17–24.

Laubinger S, Fittinghoff K, Hoecker U (2004). The SPA quartet: a family of WD-repeat proteins with a central role in suppression of photomorphogenesis in *Arabidopsis. Plant Cell* **16**, 2293–2306.

Lidon FC, Ramalho JC (2011). Impact of UV-B irradiation on photosynthetic performance and chloroplast membrane components in Oryza sativa L. *Journal of Photochemistry and Photobiology B: Biology* **104**, 457–466.

Lidon FC, Teixeira M, Ramalho JC (2012). Decay of the chloroplast pool of ascorbate switches on the oxidative burst in UV-B irradiated rice. *Journal of Agronomy and Crop Science* **198**, 130–144.

Oravecz A, Baumann A, Máté Z, Brzezinska A, Molinier J, Oakeley EJ, Adám E, Schäfer E, Nagy F, Ulm R (2006). Constitutively Photomorphogenic1 is required for the UV-B response in *Arabidopsis. Plant Cell* **18**, 1975–1990.

Rizzini L, Favory JJ, Cloix C, Faggionato D, O'Hara A, Kaiserli E, *et al.* (2011). Perception of UV-B by the Arabidopsis UVR8 protein. *Science* **332**, 103–106.

Rozema J, Staaij JV, Bjorn LO, Caldwell M (1997). UV-B as an environmental factor in plant life: stress and regulation. *Trends in Ecology & Evolution* **12**, 22–28.

Savitch LV, Pocock T, Krol M, Wilson KE, Greenberg BM, Huner NPA (2001). Effects of growth under UV-A radiation on CO_2 assimilation, carbon partitioning, PSII photochemistry and resistance to UV-B radiation in *Brassica napus* cv. Topas. *Australian Journal of Plant Physiology* **28**, 203–212.

Singh VP, Srivastava PK, Prasad SM (2012). Differential effect of UV-B radiation on growth, oxidative stress and ascorbate-glutathione cycle in two cyanobacteria under copper toxicity. *Plant Physiology and Biochemistry* **61**, 61–70.

Srivastava PK, Singh VP, Prasad SM (2014). Low and high doses of UV-B differentially modulate chloropyrifos-induced alterations in nitrogen metabolism of cyanobacteria, *Ecotoxicology and Environmental Safety* **107**, 291–299.

Stafford HA (1991). Flavanoid evolution: an enzymic approach. *Plant Physiology* **96**, 680–685.

Tian J, Yu J (2009). Changes in ultrastructure and responses of antioxidant systems of algae (Dunaliella salina) during acclimation to enhanced ultraviolet-B radiation. *Journal of Photochemistry and Photobiology B: Biology* **97**, 152–160.

Tilbrook K, Arongaus AB, Binkert M, Heijde M, Yin R, Ulm R (2013). The UVR8 UV-B Photoreceptor: Perception, Signaling and Response. *American Society of Plant Biologists* doi: 10.1199/tab.0164

UNEP (2002). *Executive summary. Final of UNEP/WMO Scientific Assessment of Ozone Depletion: 2002.* Prepared by the Scientific Assessment Panel of the Montreal Protocol on Substances that Deplete the Ozone Layer. UNEP, Nairobi.

Velders GJM, Andersen SO, Daniel JS, Fahey DW, McFarland M (2007). The importance of the Montreal Protocol in protecting climate. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 4814–4819.

Vincent WF, Roy S (1993). Solar ultraviolet radiation and aquatic primary production: damage, protection and recovery. *Environmental Reviews* **1**, 1–12.

Wu D, Hu Q, Yan Z, Chen W, Yan C, Huang X, Zhang J, Yang P, Deng H, Wang J, Deng X, Shi Y (2012). Structural basis of ultraviolet-B perception by UVR8. *Nature* **484**, 214–219.

Zhao D, Reddy KR, Kakani VG, Read J, Sullivan J (2003). Growth and physiological responses of cotton (*Gossypium hirsutum* L.) to elevated carbon dioxide and ultraviolet-B radiation under controlled environment conditions. *Plant, Cell & Environment* **26**, 771–782.